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Identity and Host Relations of Nectria Species Associated with Diseases of Hardwoods in the Eastern States[1]

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In 1936, Spaulding, Grant, and Ayers (23) summarized certain investigations of the *Nectria* diseases of hardwoods in New England, giving an account of the results of their cross-inoculation experiments and studies on the fruiting of *Nectria* fungi on diseased trees that had received various treatments possibly applicable in forest stand-improvement work. They discussed canker of various species, and the bark disease of beech, which is associated with infestations of the beech scale insect, referring to one of two species of *Nectria* in association with the latter disturbance as "number 1," and to the other, which they considered to be the *Nectria* responsible for canker on all susceptible hosts, as "number 2."

In the laboratory studies connected with these investigations and several supplementary series of cross-inoculations, together with the identification of many specimens received, *Nectria* fungi from 17 States and several Canadian Provinces were studied systematically with a cultural classi-

[1] The work herein reported was carried out largely in cooperation with Emergency Conservation Work and Civilian Conservation Corps, as a corporate part of the investigations of *Nectria* diseases of hardwoods reported by Spaulding, Grant and Ayers (23) in 1936. Cooperation and assistance are acknowledged therein. Cooperation with Osborn Botanical Laboratory, Yale University, is also acknowledged. In addition, the authors acknowledge the work of the following: T. T. Ayers, who made the initial mycological studies in 1933; G. H. Hepting, for his unpublished observations on canker-*Nectria* fungi of the Appalachian Regions; T. J. Grant, J. R. Hansbrough, and Perley Spaulding, for additional collections of *Nectria* in 1935 and 1936, essential to the host-region sampling project upon which the mycological studies were concluded.

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fication of 605 of the specimens that were entered in the Herbarium of the Division of Forest Pathology, representing more than 30 host species, and observations on approximately 3,000 additional cultures in connection with experimental work. The purpose of this paper is to present the morphologic and cultural aspects of the Nectrias referred to above as numbers 1 and 2, as we have studied the species from various areas in New England and in comparison with similar or closely allied Nectrias from other regions in the East.

The literature on *Nectria* fungi associated with canker of hardwoods in Europe and North America is replete with unavoidably tentative determinations, questionable application of names, inadequate descriptions, and many pages of controversial discussion on the specific identity and pathogenicity of forms studied. This is due to variations in usage of species names, to lack of knowledge of the distribution of species, and to conflicting interpretations as to the diagnostic value and variability of such features as color and shape of perithecia, structure of perithecial wall, shape of ascus, size, shape, and ornamentation of ascospores, size and shape of microconidia and macroconidia, general and special cultural characteristics, and pathogenicity, especially as determined by inoculations. With respect to the literature, the present paper includes only a brief outline of the more important articles that bear directly upon the nomenclature of the canker Nectrias and a short review of the *Nectria* canker diseases that occur in the eastern States.

THE NOMENCLATURE OF CANKER-FORMING SPECIES ON HARDWOODS

The *Nectria* in association with canker of hardwoods was first referred to *N. ditissima* Tul. by Hartig (13) and Goethe (9) in Europe, and by Galloway and Woods (8) in the United States. Later it was reported in this country as *N. coccinea* Pers. ex Fr., by Pollock (18), and in Europe as *N. galligena* Bres. by Weese (26, 29), who redescribed that species and reiterated his opinion that *N. ditissima* must be considered a synonym of *N. coccinea*.[4] Subsequently, the history of these fungi in European literature becomes highly controversial with respect to the application of the three names in consideration of both the morphological features and the host relations ascribed to each. In American literature during the past twenty years, the names have received about equal usage, although, since Wollenweber (33) identified perithecia on cankered apple from Massachusetts as *N. galligena*, that name has been applied rather consistently in reports of canker on pomaceous hosts. *N. coccinea* (15), *N. ditissima*

[4] The Tulasnes (25) proposed *N. ditissima* as a new species presumably because of apparent confusion over *N. coccinea* Pers. ex Fr., due in part to the fact that specimens believed to be Persoon's *Sphaeria coccinea* did not conform to the notation by Fries (7). It cannot be determined whether these Nectrias of the Tulasnes and Persoon are identical.

(40), and *N. galligena* (1, 3) are used currently in connection with canker on various other hardwoods.

The nomenclature of these fungi, in brief, is a matter of usage, both past and present, both in pathological literature and in current systematic treatments, showing conflicting opinions with respect to *ditissima* versus *coccinea*, *galligena* versus *ditissima*, and *punicea* versus *coccinea* and *ditissima*. To appreciate the present confusion it is necessary only to refer to a recent paper by Petch (17) and to the detailed discussions on the provoking nomenclatorial history of the species as given by Westerdijk and Van Luijk (32), Richter (20), and Ashcroft (1).

NECTRIA CANKER DISEASES AND FRUITING HABITS

In hardwoods, *Nectria* fungi are responsible for diseases termed dieback in the case of twig infections and canker in the case of branch and stem infections that exhibit localized necrosis of bark and cambium. Dieback is generally considered to be of minor importance in forest stands, regardless of the species of *Nectria* concerned, although there is an increasing amount of circumstantial evidence, reviewed by Grant and Spaulding (11), indicating that perennial branch cankers caused by the canker *Nectria* [*N. galligena*] alone in many instances may have their inception in this condition. The *Nectria*-canker disease has been shown to be widespread and serious in certain hardwood stands of New England (23, 30, 31) and farther South (1, 12, 14). The general history of this disease is given by Zeller (39) and Ashcroft (1), and for some of the forest species variations in configuration of cankers as related to host morphology are discussed by Welch (31) and Grant (10). Since both canker and dieback have been termed canker in the earlier literature, and since the taxonomy of the species of *Nectria* associated has been very unsatisfactory, canker of forest trees has been recorded for the United States in connection with *Nectria cinnabarina* Tode ex Fr. (*Creonectria purpurea* (L.) Seaver), *N. coccinea* Pers. ex Fr. (*Creonectria coccinea* (Pers.) Seaver), *N. ditissima* Tul., *N. galligena* Bres., and *N. sanguinea* Sibth. ex Fr. It is highly probable that but one species, *N. galligena*, has been responsible for the disease in all reports that have dealt with perennial cankers, characterized by repeated localized destruction of phloem and cambium on eastern hardwoods other than *Sassafras*, *Liriodendron*, and certain species of *Magnolia* (see diagnoses and discussions of species to follow below). Cankering of exotic hardwood species by *Nectria cinnabarina* is rare.

In the study of the canker disease in the East, Welch (31) and Spaulding et al. (23) gave attention to perithecial production by *Nectria* [*N. galligena*] with respect to such factors as host species, vigor, age of canker, condition and age of girdled or felled cankered stems, and the continuation or periodicity of fruiting after girdling or felling. These authors concluded that

perithecial production normally continues periodically as long as the moisture supply in the infected tissues is favorable, even from 12 to 30 months after the death of the host. They found little or no evidence of perithecial production that might be due to new infections of dead tissues, or to a continued extensive invasion of such tissues from the mycelial region of the original canker. They also concluded that the copious ascospore production by such fruiting upon dead, standing, or fallen infected stems augments very successfully the conidial and perithecial fruiting on living stems in providing inoculum for natural infections. Probable mycelial growth in forest litter and subsequent conidial production therein from this abundant spore population was not investigated. The identity of the fungus involved in the prolonged fruiting on dead materials as the active canker *Nectria* has been investigated by Welch (31), Spaulding et al. (23), and repeatedly by us for a number of hosts in the present study. That cultures of the *Nectria* in this stage of belated fruiting are pathogenic has been demonstrated particularly in the case of fruiting on beech and birch, in several series of inoculations in New England, including those reported by Spaulding et al. (23).[5]

In certain areas of New England and the Canadian Maritime Provinces, American beech is cankered by a *Nectria* fungus that appears to follow infestations of the beech scale insect. The most commonly observed lesions in this disease, at the time that the *Nectria* stromata are producing either macroconidia or perithecia on bark still intact, are circular patches up to about 2 cm. in diameter, flat or somewhat sunken, scattered or coalescent and typically separated in age from the surrounding healthy bark by a marginal crack. These lesions, especially when coalescent and accompanied by drying, cracking, and loosening of the bark, are most characteristic of the advanced stages of the decadence that Ehrlich (6) has described as the beech bark disease. Beech in certain areas is deformed by deeper cankers with erect or inwardly arched walls of smooth callus. These may occur alone or intermingled with the above-mentioned lesions. Ehrlich (6, p. 617) interpreted them as instances of the *Nectria* infection being healed out. He attributed the cankering in the bark disease to an unnamed variety of *Nectria coccinea*.

In 1933 Ayers determined the presence of two types of *Nectria* on scale-infested beech. These, as previously reported by Spaulding et al. (23), he classified as number 1, or Ehrlich's *Nectria*, and number 2, a *Nectria* that he characterized as having typically larger ascospores and rather distinctive, although variable, cultural characteristics and that appeared to

[5] Reference is to field inoculations of the following series: 1933 at Winthrop, Maine; 1934 at Cherry Mountain, New Hampshire; 1935 at Winthrop, Maine and Cobalt, Connecticut. These studies were carried out under the supervision of Perley Spaulding, with T. T. Ayers, T. J. Grant, J. R. Hansbrough, and M. L. Lohman participating.

be more or less in agreement with the *Nectria* found associated with cankers of other host species in New England. In 1936, Spaulding, Grant, and Ayers (23) presented quantitative estimates of the relative abundance of *Nectria* numbers 1 and 2 on diseased and healthy beech in sample plots in eastern Maine. They observed that of the two forms of *Nectria* the number 1 was typically much more abundant, that both were present on a few trees on which the scale insect had not been observed, that both Nectrias more readily attack the weakened bark of scale-infested trees than the healthy bark of uninfested trees, and that the number 2 *Nectria* was of much wider distribution, being present in 21 of 23 sample plots, as compared with number 1 *Nectria* in only 8 of the plots.

From these reports it appears that the aspects of individual *Nectria* lesions on American beech depend upon the characteristics of the bark as determined by age and vigor of the tree, kind of *Nectria* present and its virulence and, more particularly when the scale insect is involved, upon the age and degree of its infestation.

THE SPECIFIC IDENTITY OF CERTAIN NECTRIAS PATHOGENIC TO EASTERN HARDWOODS

Throughout the present study specimens have been referred to numbered groups on the basis of (a) *perithecial habit* in field samples and in fruiting following artificial inoculations in the field, (b) *mean size of ascospore*, and (c) *macroscopic cultural characteristics*, or on the basis of only the first and second or first and third of these aspects. The probable validity of the groupings has been verified as follows: (1) By analyses of data on size of ascospores; (2) by measurements of conidia in selected cultures; and (3) through a further comparison of selected cultures by their relative tolerance of malachite green, and (4) by the presence or absence of hyphal fusions in pairs of selected cultures. *Nectria* number 1 of American beech is identified as an unnamed variety of *N. coccinea* Fr., *sensu* Wr. (34), and its segregate, which was found among living specimens only on *Acer saccharophorum* Koch, as the species. Number 2 is identified as *N. galligena* Bres. and its segregate on *Liriodendron* and species of *Magnolia*, as an undescribed species which, in comparison with *N. galligena*, has ascospores of similar form but smaller, is distinct in conidial aspects, is slightly but consistently different in cultural habit, and apparently is adapted as a canker-forming parasite only to certain species of the Magnoliaceae. A second segregate is *N. mammoidea* Phill. & Plowr., which is equally closely related but is distinct in the multiple structure of the perithecial wall, cultural characteristics, and macroconidia. These Nectrias are diagnosed briefly in Table 1 and, with the exception of *N. mammoidea*, they are compared graphically in Fig. 2 with respect to variation in mean size of ascospores among samples from the various tree species.

TABLE 1. *Synopsis of the more important species of Nectria studied culturally in the investigation of Nectria-canker diseases of eastern hardwoods. Descriptions are given in the text.*

Species	*Nectria galligena* Bres. Fig. 1, G, H and I, and 2, A, B, C, and D	*N. magnoliae* Fig. 1, C and D, and 2, D	*N. mammoidea* Phill. and Plowr. Fig. 1, E and J	*N. coccinea* Fr. *sensu* Wr. Fig. 1, F and 2, B	*N. coccinea* var. *faginata* Fig. 1, A and B, and 2, C
OCCURRENCE	On bark, callus, or wood of living or dead (recently felled) stems; the common perennial canker fungus of various hosts, except *Ranales* and certain other orders	On bark, less often on callus or wood of living or dying or fallen stems; the common cause of *Liriodendron* and *Magnolia* cankers	On bark, callus, and wood of living or felled stems: *Quercus* and *Betula*	On bark of girdled or felled stems: *Acer saccharophorum*	On weak or dying bark, especially following attack of European beech scale insect: *Fagus grandifolia*
PERITHECIA (dry field samples)	Orange, then red or bright reddish-brown; *apex sometimes circumscribed;* single or in small groups of 2–8 on thin stroma; colored medial wall cells uniform, tending to elongate-angular	Pale orange, then reddish-brown, brownish-drab, or blackish-brown; *smaller than in N. galligena;* single or in small groups of 2–12 on thin stroma; wall cells as in *N. galligena*	Orange, then reddish-orange or purplish red; *apex flattened-circumscribed, strongly papillate;* single or in groups of 2–20 on thick stroma; *colored medial wall cells biform* (see explanation in text)	Reddish-orange, then bright red, then reddish- or brownish-drab; single or in *groups of 2–30* (or more by coalescence of groups) on thick stroma; colored medial wall cells uniform, tending to oblong or elongate-angular	Reddish-orange or bright red, then reddish- or brownish-drab; in groups of 7 to 15 or, by coalescence, of 20 to 35 or more, on thick stroma; wall cells as in *N. coccinea*
ASCI (tip)	Rounded, then *usually broadly* rounded	Truncate, or subtruncate, then narrowly rounded	As in *N. magnoliae* but much larger	Broadly truncate, then subtruncate-rounded	As in *N. coccinea*
ASCOSPORES (for field samples) (size in μ)	Ellipsoidal or broadly fusoid: 11–25×4–9, normally 13.4–19.4×5.7–7.9 averaging 16.4×6.7	*Form as in N. galligena;* 9–16×4–7, normally 11–15.1×4.7–6.1 averaging 13.1×5.4	*Typically fusoid, unequal-sided* but variable (see text); 14.2–24.2×5.8–8.6, normally 15–24×6.2–8.0 (for averages see table 2 and discussion in text)	Ellipsoidal or with ends more obtusely rounded, especially the upper; 10.2–15.4×4.6–7.2, normally 11.9–13.9×5.6–6.4 averaging 12.8×5.8 (however, see text)	Ellipsoidal to broadly ellipsoid; 8–18×4–7, normally 11–13.6×5.2–6.7 averaging 12.35×5.96
CONIDIA (from cultures) (normal size in μ)	0- to 8-septate 0-) elliptic-oblong in outline, 7.8–11.9×3.8–4.5 5-) *cylindric clavate and nearly straight* 44–58×5.9–6.8	0- to 6-septate 0-) elliptic-oblong in outline or suballantoid, *6.2–7.8×1.8–2.8* 5-) cylindric fusoid, *moderately curved* 52–62×4.5–5.5	0- to 5-septate 0-) long ellipsoidal, very rare, 15×3.5 5-) *broadly subcylindric, slightly curved*, the ends sometimes more strongly curved 42–63×5.4–6.8 (see table 2 and discussion in text)	0- to 6-septate 0-) ovoid unequal-sided, or long ovoid, or elongate ellipsoidal, 4.7–11.8×2.0–4.2 5-) thick cylindric fusoid, moderately curved 44–48×5.6–6.2	0- to 8-septate 0-) elongate ellipsoidal, sometimes unequal-sided or suballantoid, 8–14.8×2.2–3.8 5-) elongate subcylindric, moderately curved *58–82×6.8–7.6* (however, see discussion in text)
REACTION TO MALACHITE GREEN: Dye tolerance index (p.p.m.)	1.8–16.0	4.2–11.0	270–700	1.5–2.8	1.6–2.3
REACTION TO MALACHITE GREEN: Colony diameter on control medium (cm.)	7.0	8.8	4.7	9.1	7.5

MATERIALS AND METHODS

Ascospore measurements.—From 483 field collections for each of which lengths and widths of 25 or more ascospores had been recorded, 235 collections with measurements of 10,580 ascospores were selected for bio-

metrical analyses to be representative of the various tree species in diverse geographical areas in the eastern States. The selection provided five or more samples for each of 13 tree species; fewer samples for 17 additional species; and in the case of the more commonly infected hosts such as beech, maples, and birches, an equal degree of sampling for each of several geographical areas. All measurements were made with the same microscope, provided with a filar micrometer, and fixed collar. To assure a systematic survey of the field of spores a mechanical stage was employed. In much of the later work 25 ascospores were measured for each collection since an inspection of measurements for samples of 100 spores each indicated that the smaller sample was satisfactory. The measurements were made from permanent slides, the majority of which were prepared by the eosin-glycerin method. The one or more slides for each field sample represented a mixture of 8 to 10 perithecia taken from different portions of the specimen.[6] In a small number of field samples in the preliminary work measurements were made of spores in a solution of cotton blue in lactophenol. In order to broaden the host range in the sampling, some of these measurements were included in the analyses, but only after it was determined that the method of mounting the spores did not significantly alter the spore measurements. Approximately 1,000 measurements were made in all to clarify this point.

In the analysis of ascospore measurements by groups or species, with the exception of the data for *Nectria coccinea* and *N. mammoidea*, for which insufficient specimens were available, measurements were treated by standard statistical methods, in general as employed by Colley (4) and Colley, Hartley, and Taylor (5) for the determination of comparable group constants. Of these data, only mean length and width, and standard and extreme ranges in length and width are incorporated in the descriptions below. Both the mean and extreme sizes were determined to facilitate comparisons with published data wherein various methods of summarization have been employed, especially in the critical studies of hardwood Nectrias in Europe.

Laboratory cultures.—Nectrias from several thousand specimens, including the greater part of those for which ascospores were measured, were obtained in pure culture from ascospores removed singly or in small groups from nutrient-agar plates. In the reisolations from field inoculations and the cultural determination of *Nectria* in association with the bark disease of beech and canker on treated trees, a larger number of cultures were obtained for temporary study by isolations from infected host tissue, from conidial stromata, or from perithecia surface-sterilized with 95 percent alcohol. Cultural groupings were determined from characteristics on either

[6] Mounts were prepared by treating perithecia with 95 percent alcohol (about 5 minutes), 2 percent KOH (same), distilled water (1 minute), 1 percent aqueous eosin (10 minutes or more), 3 percent acetic acid (same), and then glycerin added. Subsequently, the material was teased apart thoroughly to secure an abundance of free ascospores.

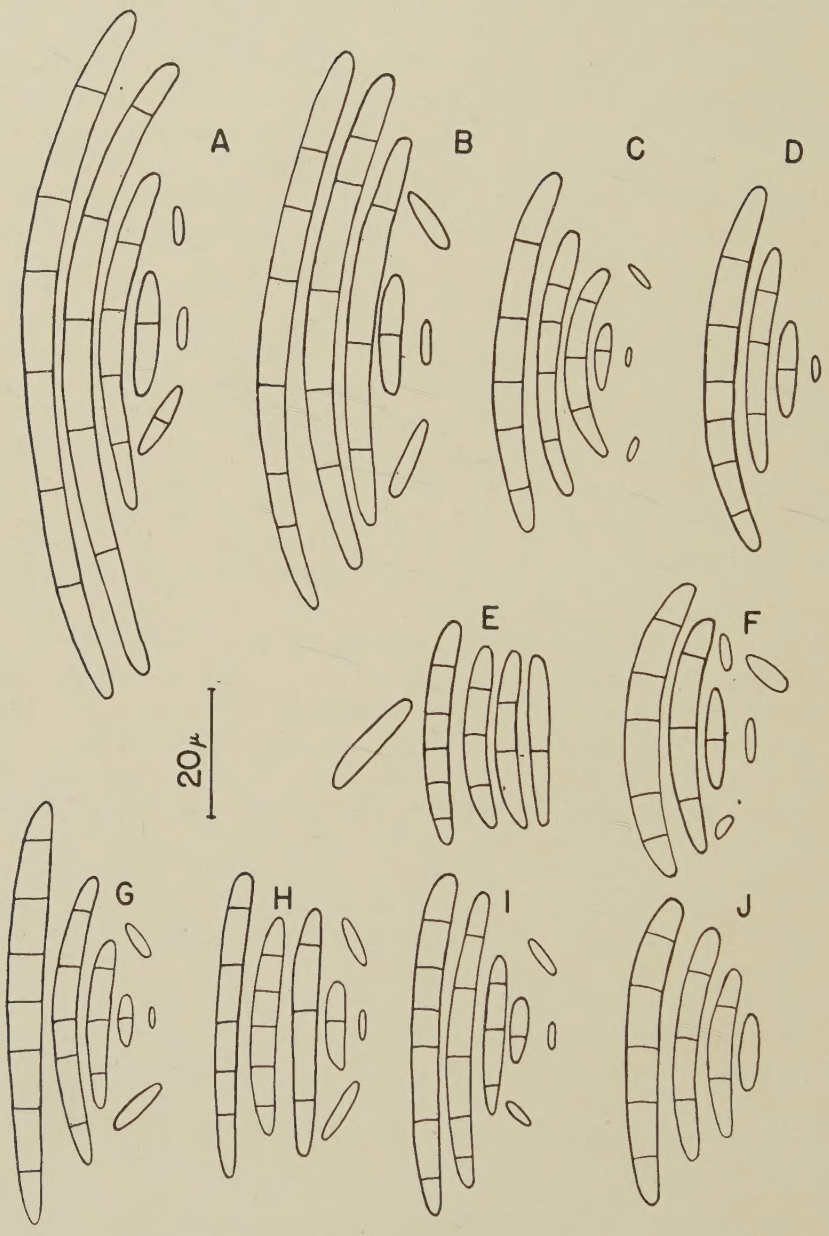

FIG. 1. Macroconidia and microconidia of *Nectria* species in culture: *A* and *B*, *Nectria coccinea* var. *faginata*; *C* and *D*, *N. magnoliae*; *E*, *N. mammoidea* (culture No. 69675); *F*, *N. coccinea*; *G–I*, *N. galligena*; *J*, *N. mammoidea* (culture No. 69610).

potato-dextrose or synthetic bacto-malt agar media, or both.[7] Attention was given to coloration in the aerial, surface, and subsurface layers and to colony type, with emphasis on the former. Records on conidial development were obtained at various intervals for many of these cultures, all of which were held in diffuse daylight at room temperature. Culture groupings were made largely on the basis of the degree of development and coloration of the surface layer and the characteristics of the aerial mycelium, features which to a certain extent are correlated with conidial types.

Special differential culture studies.—Fifty-two cultures, representing as many field samples, were selected on the basis of their grouping by ascospore measurements and general cultural characteristics for testing their tolerance of malachite green in a synthetic nutrient agar medium especially favorable for mycelial growth.[8] The dye in aqueous solution was added to the medium before autoclaving in amounts sufficient to give seven concentrations varying from 2.5 to 500 parts per million. In the experimental series plate cultures were run in triplicate, beginning with inocula of equal size transferred from vigorous plate cultures, of like age and of second or third subculturing on the control medium. Average colony diameters, the mean of major and minor diameters, were recorded on the tenth and fifteenth days. For each isolate the mean of the measurements at the two times was determined for each concentration and expressed as a percentage of the growth on the control medium. From these percentages graphed over the logarithms of the concentrations there was determined the amount of dye required to reduce growth 75 percent and this amount was taken as the dye-tolerance index for the isolate. Observations also were made on the degree to which the dye was removed from the medium and concentrated in the mycelium.

Selected cultures were also grown on steam-sterilized elm and yellow-poplar twigs in water agar, on moist steam-sterilized rice, and on oatmeal agar, either for the study of macroconidia or for comparing certain "light" and "dark" cultural types within both the *Nectria coccinea* and N. *galligena* culture groups.

A selection of 52 cultures was used in the investigation of sample-specimen and group relationships as determined by the presence or absence of hypha-to-peg and peg-to-peg fusions in paired cultures on a malt agar medium.[9] In this selection 38 cultures represented specimen samples that

[7] Potato-dextrose medium: Liquid from 250 gr. peeled potatoes boiled 1 hr.; dextrose 20 gr.; glycerin 20 gr.; agar 20 gr.; distilled water to make 1 liter.

Synthetic bacto-malt medium: Maltose (technical) 12.75 gr.; dextrin 2.75 gr.; glycerin 2.35 gr.; peptone 0.78 gr.; agar 20 gr.; distilled water 1,000 ml.

[8] The stock nutrient and control medium in dye-tolerance studies: $MgSO_4 \cdot 7H_2O$, 2.85 gr.; KH_2PO_4, 1.67 gr.; $Ca(NO_3)_2 \cdot 4H_2O$, 2.86 gr.; peptone, 1.0 gr.; maltose, 10 gr.; dextrin, 5 gr.; glycerin, 10 gr.; agar (bacto), 20 gr.; distilled water to make 1 liter.

[9] Medium used in anastomosing studies: Maltose (technical) 4 gr.; Keplar's Liquid Malt 20 gr.; agar (bacto) 25 gr.; distilled water 1,000 ml.

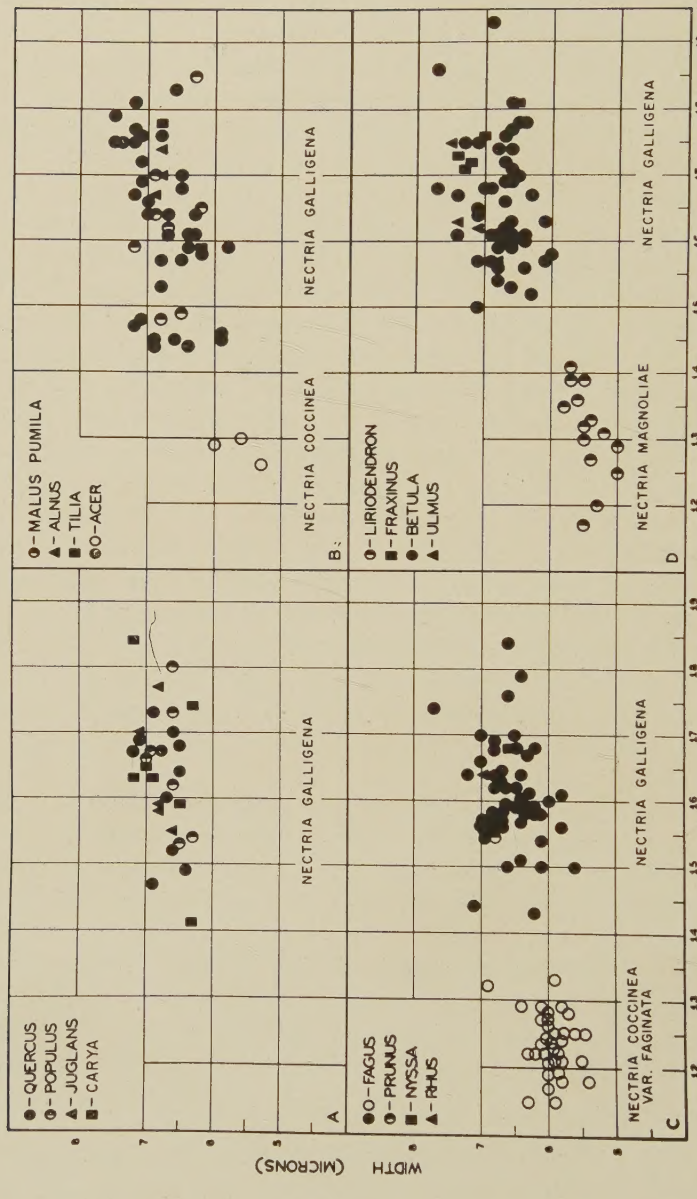

FIG. 2. "Scatter" diagram of the population of ascospores of *Nectria* species, plotting mean length against mean width for each of the samples collected from the various hardwood host species. (Drawn by Harold Eno.)

had been used in the biometrical studies. The additional 14 cultures represented other fungi including *N. mammoidea*, *N. episphaeria* Tode ex Fr., and *N. cucurbitula* Tode ex Fr. Of the 52 cultures, 28 were represented in the selection for dye-tolerance studies. Mycelial transfers of cultures being paired were made to plates containing the nutrient agar sufficient to cover by a thin film a sterilized microscopic slide, in such manner that the advancing margins of the opposed cultures would meet over the slide. When microscopic examination at low magnification showed an intermingling of the two mycelia, the slides were removed and flooded with a solution of cotton blue in lactophenol. Thin cover glasses were applied and after the mounts had cleared a systematic study at high magnification was made with the aid of a mechanical stage. Altogether, 166 different combinations were studied, the selections being made so as to reveal the specific unity of subgroups and groups as well as intergroup reactions.

Conidial stages.—Permanent slides as prepared in the study of ascospores were used for measuring macroconidia taken largely from the cultures of ascosporic origin. Lengths and widths, and the degrees of septation were recorded for 25 or more conidia from each isolate. Means were not calculated, the comparisons being made on extreme and normal ranges in size for septation classes. Microconidial and macroconidial development also was observed in connection with the dye-tolerance and hyphal-fusion studies and for selected cultures grown on steam-sterilized elm and yellow-poplar twigs in water agar. The conidia were measured by the method used for ascospores.

DESCRIPTION AND DISCUSSION OF NECTRIA SPECIES

1. Nectria galligena Bres.

Perithecia superficial, more conspicuous on exposed inner bark and callus tissue of stems, single or forming small, loose, irregular clusters of 2 to 8, sometimes by renewed fruiting and coalescence of groups in fissures of bark, densely gregarious to subcespitose, not uncommon but less conspicuous when single or scattered on blighted twigs, on bud-scale scars, and on firm wood recently exposed by pruning and coppice cutting—when clustered, seated upon a thin, irregular, orange stroma with fimbriate or lacerate margin, more or less erumpent through outer bark—conic-ovoid to broadly pyriform and variably papillate-ostiolate, occasionally collapsing from above when immature or unilaterally when spent, at first orange-colored, then more brownish or reddish and usually with slightly darker papillum, finally reddish-brown, dark red, sometimes slightly purplish-red, generally 250–425×200–380μ, the walls parenchymatic or nearly so, 13–50μ thick, variably radially prosenchymatic above, the colored cells below usually elongate-angular in vertical sections; asci 8-spored, broad-cylindric, then clavate, 85–105×10–14 (16)μ, broadly conate or rounded

above with the upper spore appressed, short-stipitate, tufted and paraphysate; paraphyses sparse but persistent, exceeding the asci, moniliform, tapering, thin-walled and with basal cells greatly swollen; ascospores at first uniseriate, usually becoming irregularly subbiseriate above, ellipsoidal or broadly fusoid with rounded ends, hyaline or sometimes with faint yellowish cytoplasm, smooth or occasionally minutely punctated, the two cells equal or nearly so in unconstricted and constricted spores, (11)13.4–19.4 (25)×(4)5.7–7.9(9)μ, averaging 16.4×6.7μ.[10]

Cultural characteristics.—On synthetic malt agar medium the aerial mycelium floccose, with or without zonations, white to light cinnamon or buff (Light Buff);[11] surface mycelium sometimes undifferentiated, usually well-developed, stromatic, chalk to brownish (Cinnamon, Cinnamon-Buff, Tawny, or Prout's Brown); on potato dextrose agar the aerial mycelium cottony to floccose, white to light cinnamon brown (Ochraceous-Tawny, Cinnamon, or Cinnamon-Brown); surface mycelium usually better developed than in malt agar cultures and darker (Ochraceous-Tawny to Buckthorn Brown, Dresden Brown, or Auburn); upon either medium the subsurface coloration usually either somewhat lighter or darker than the stromatic layer, tending to disappear in old cultures; perithecial production very infrequent and macroconidial columns lacking.

On steamed rice the aerial mycelium white, velvety, conspicuous; surface mycelium soon with shades of yellow or pale greenish-buff (Citron Yellow, Light Cadmium, Empire Yellow, Cadmium Yellow, Colonial Buff, and Deep Colonial Buff) in some cultures remaining so, in others becoming yellowish or brownish-olivaceous (Reed Yellow, Olive-Buff, Deep Olive-Buff and Olive-Yellow), occasionally with areas of rich brown (Dresden Brown).

On the malachite medium mycelia tolerant of low and medium concentrations of dye, typically showing moderate degrees of absorption; the usual range in index values 2.6–12.5 and the extreme, 1.8–16.0 p.p.m.; average colony diameter on the control medium, 7.0 cm.

Conidial stages (Fig. 1, G–I)—*Cylindrocarpon mali* (Allesch.) Wr., *C. mali* var. *flavum* Wr., *C. willkommii* (Lindau) Wr. and *C. willkommii* var. *minus* Wr.—Conidia variable in size and number of septations, with apex obtusely rounded and base broadly conical to subtruncate, in mass chalk white, cream, yellowish-green or tan, appearing on bark as powdery masses or minute sporodochia, in cultures as a uniform or subzonate dust, as scattered powdery masses, erumpent glistening droplets, or as firm dull knobs

[10] The figures in parentheses in measurements of asci, ascospores, and conidia are extreme values. When not so indicated or otherwise referred to as extreme, values indicating ranges are expressions of the normal or usual range as determined by mere inspection of data, except in the case of ascospore measurements of *Nectria galligena*, *N. magnoliae*, and *N. coccinea* var. *faginata* wherein the values express a standard range with limitations three times the standard deviation of individual ascospore means above or below the mean for the species.

[11] Color terms in parentheses are those of Ridgway (21).

of massed sporodochia depending upon culture conditions, and in the young growth of darker colored cultures the microconidia frequently being agglutinated into microscopic false heads on scattered simple conidophores; when continuous, elliptic-oblong—when sparingly septate, thick-clavate or inequilateral—when pluriseptate, occasionally elongate-fusiform but usually cylindric-clavate and nearly straight; in general 0- to 8-septate, measuring 4.8–110×2.6–8.4μ and, among several-celled conidia either the 4-, 5-, or 6-septate condition predominating in a single culture; conidiophores simple or subverticillate.

The following measurements for standard conidial types are the extreme and usual limits for samples of 25 conidia each from ascospore cultures of different origin grown for 4 weeks on oatmeal agar at approximately 20° C. and selected to represent the full range of the species as described above with respect to ascospore size and cultural characteristics: 0–(9 cultures for 6 host species):(4.8)7.8–11.9(18.4)×(2.6)3.8–4.5(5.2)μ; 3–(25 cultures for 12 host species): (22)29–40(50)×(3.8)5.3–6.4(7.8)μ; 5–(25 cultures for 12 host species): (35)44–58(70)×(4.6)5.9–6.8(7.8)μ; 7–(5 cultures for 5 host species): (61)72–79×(5.0)5.4–6.4(7.0)μ.

Specimens studied culturally and biometrically with respect to ascospores represent collections from the following host species in various localities of the northeastern and Allegheny forest areas: *Acer pensylvanicum* L., *A. rubrum* L., *A. saccharophorum* Koch, *A. spicatum* Lam., *Alnus incana* (L.) Moench., *Betula lenta* L., *B. lutea* Michx., *B. nigra* L., *B. papyrifera* Marsh., *B. populifolia* Marsh., *Fagus grandifolia* Ehrh., *Fraxinus nigra* Marsh., *Carya tomentosa* (Lam.) Nutt., *C. cordiformis* (Wangh.) K. Koch, *C. glabra* (L.) Sweet, *Juglans cinerea* L., *J. nigra* L. (also from Ohio), *Malus pumila* Mill., *Nyssa sylvatica* Marsh., *Populus grandidentata* Michx., *P. tremuloides* Michx., *Prunus serotina* Ehrh., *Quercus alba* L., *Q. bicolor* Willd., *Q. borealis* Michx. f., *Q. borealis maxima* (Marsh.) Ashe, *Q. coccinea* Muench., *Rhus typhina* L., *Tilia americana* L., and *Ulmus americana* L.[12] The majority of the specimens were collected from cankered stems (23); some, however, were taken either from the bark in areas adjacent to cankers or from cut surfaces of bark and sapwood, exposed on girdled or felled trees, and from galls on branches of *Carya cordiformis*, *C. glabra*, and *Fagus grandifolia*. In the case of beech, most specimens are from smooth bark or from cracks and chinks in smooth bark; with a few either from the old bark in pits or wells on diseased stems or from cuts through sapwood on standing or recently felled trees. The species is most frequent on bigtooth aspen, American beech, and the several species of birch and maple, but its relative abundance on any host varies with the climatic conditions of the forest area. Largely as delimited above, the host relation-

[12] The scientific names of trees throughout this paper are according to the International Rules of Nomenclature, and the common names are after Sudworth (24).

ships of this species in New England have been discussed in detail by Spaulding, Grant, and Ayers (23).

Although not included in the present study, the *Nectria* fungi in association with canker on *Prunus pensylvanica* L. (11, 30, 31), *Amelanchier laevis* Wieg., and undoubtedly on certain other tree species listed by Welch (30, 31), are *N. galligena*. Likewise to be included are specimens from cankered tissue showing perithecia more densely cespitose, and minutely verrucose, with strongly papillate, flattened, blackish tops as in No. 56959 (labelled *Creonectria mammoidea* (Phill. & Plowr.) Seaver) from *Juglans nigra*, Alta (? Alta Vista), Virginia, and No. 70918 from *Quercus coccinea*, Oakland, Maryland.[13]

Whereas in Europe Wollenweber (35, 36) and Richter (20) have attempted to show specific and varietal differences among specimens in association with canker on trees of different host genera, among our specimens no variety clearly distinct in morphology or pathogenicity is apparent. In culture, however, the *Nectria* of *Fraxinus nigra* in New England is fairly distinctive in coloration, the golden brown to reddish shades of the surface layer and the subsurface coloration being richer than in some of the isolations from species of *Carya*, *Juglans*, and *Acer*, which, for the most part, account for the darker colorations in the foregoing description. The aerial mycelium is buff to light brown (Pinkish Buff to Cinnamon-Buff and Tawny-Olive) on the malt medium and white to light brownish (Ochraceous-Tawny and Cinnamon) on the potato dextrose medium. The stromatic layer and subsurface coloration are brownish (Saccardo's Umber to Bister and Sepia) on the former medium and reddish-brown (Buckthorn Brown to Auburn) on the latter. These are approximately the colorations upon which Wollenweber and Richter recognize *N. galligena* var. *major* Wr., on *Fraxinus* in Europe, as distinct from *N. galligena* on other hosts. The *Nectria* of black ash in New England is identifiable as this variety with respect to other taxonomic features, particularly the size of ascospore and size and septation of conidia. However, the variety could be recognized only on its host specificity and coloration in culture, for certain specimens from wild apple, paper birch, and swamp white oak in New Hampshire and from sweet birch in West Virginia have equally large macroconidia and for all but the last-named host, equally large ascospores, but the cultures of these are typical *N. galligena*. None of the cultures, including those from black ash, has produced either perithecia or the occasional, short macroconidial columns, both of which were observed by Wollenweber (37) and Richter (20) in their cultures of *N. galligena* var. *major*.

In cross inoculations a culture of the *Nectria* from black ash produced unquestionable cankering on small stems, 1 to 3 inches d.b.h., of beech and

[13] Unless otherwise indicated specimen numbers refer to accession numbers in the Herbarium of the Division of Forest Pathology.

basswood but was inactive on equally small stems of red and striped maple, and white ash, and on beeches of larger diameter.[14] Comparable inoculations with cultures of *Nectria galligena* from beech on all hosts except basswood, which was not inoculated, gave equally inconclusive results, producing cankers only on stems of beech. It should be noted that the inoculations of this series were made at the time of most active stem growth and of probably the greatest potential resistance of the hosts to infection.

In the anastomosing studies hyphae of *Nectria galligena* of different cultural origin were found to fuse sparingly. In a few of the tests no fusions could be found. Still more sparingly and in a minor degree, fusions occurred in combinations between this species and *Nectria coccinea* var. *faginata*, *N. magnoliae*, and *N. mammoidea* but not with *N. coccinea*.

Nectria galligena is more closely allied with the two following species than with *N. coccinea* or any of its described varieties.

2. **Nectria magnoliae** Lohman & Hepting, sp. nov.

Perithecia subsolitaria vel gregaria, aurantiaca vel rubrofusca, postremum fusco-atra ne purpureo-coccinea, globosa vel ovoidea, leniter papillata, 200–260×175–250μ, in ligno superficialia, non stromatica, typice in stromatibus corticis erumpentibus aurantiacis; peridium pseudoparenchymaticum, 15–20μ crassum, ostiolum versus leniter radialifibratum; stroma alia plectenchymaticum aurantiacum, tenuiculum, alia nullum; asci 8-sp., cylindrico-clavati, truncati dein subtruncati vel rotundati, 75–85×6–8 (10)μ, moniliformiter paraphysati; ascosporae ultimum inordinato subbiseriatae, hyalines vel pallido flavidae, leves, ellipsoideae vel crassifusoideae, 13.1×5.4, 9–16×4–7μ, typice 11–15×4.7–6.1μ, cellula inferiora interdum angustato-elongata; mycelia culturarum prima albido-cremea dein citrino-flavida vel cinnamomea, aeria paula radialiter quasi appressata, zonata, conidifera, peritheciis raro praedita.

Status *Cylindrocarpon*.—Microconidia continua, bacillaria vel suballantoidea, 5.8–9.4×1.8–2.8μ, libera, alia in capitulis falsis disposita vel in sporodochiis flavidis tuberculariibus formata; macroconidia 4–5(3–6)-septata, elongata, modice arcuata, 44–68×4.0–6.0μ, typice 52–62×4.5–5.5μ, in sporodochiis albo-cremeis, e conidiophoris simplicibus vel subverticillate ramosis orta; chlamydosporae nullae.

Hab. in cortice truncorum et ramorum vivorum *Liriodendri* et *Magnoliae*.

Obs. Species a *Nectria galligena* Bres. differt praecipue ascosporis et microconidiis minoribus, macronconidiis non cylindraceo-clavulatis, et charact. myceliorum culturarum plus minusve *Nectriae coccineae* adfini.

[14] Reference is to a series of inoculations made by M. L. Lohman and T. T. Ayers at Winthrop, Maine, June 1935, and observed in September 1937, involving 8 *Nectria* strains, 109 inoculations, 38 control incisions, and 45 stems of seedlings or saplings of the above-mentioned species.

Type specimen: No. 64184. Cankered *Liriodendron tulipifera;* Camp Woodbine, Cranberry River, Richwood, W. Va. M. L. Lohman. Nov. 21, 1934—Mycological Collections, Bueau of Plant Industry. (Ex-type: Farlow Herbarium, Harvard University; The New York Botanical Garden; University Herbarium, University of Michigan).

The following para-type specimens accompany the type: No. 64185. Cankered *Liriodendron tulipifera;* Wolf Creek, Del Rio, Tenn. M. L. Lohman. Oct. 25, 1934.—No. 64187. Cankered *Liriodendron tulipifera;* Bent Creek Experimental Forest, Asheville, N. C. M. L. Lohman. Oct. 12, 1934.

Perithecia superficial, single and scattered to densely gregarious on exposed wood, inner bark and callus tissue, or subcespitose in small clusters of 2 to 12 or more on minute scattered to closely aggregated orange-colored stromata erumpent through the outer bark of cankered stems and branches, subspherical to obovoid when young, finally spherical or broadly ovoid, papillate-ostiolate, sometimes collapsing from above when immature and from the side when matured, yellowish or pinkish-orange, with concolorous or reddish-brown papillum, then reddish-brown, brownish or nearly black, 200–260×175–250μ walls pseudo-parenchymatic, typically 15 to 20μ thick, narrowly prosenchymatic about the ostiole; asci 8-spored, cylindric-clavate 75–85×6–8(10)μ, truncate above, becoming subtruncate to broadly rounded with the upper spore included, short-stipitate, tufted and paraphysate; paraphyses longer than the asci, moniliform, tapering, simple or branched, thin-walled and with basal cells swollen; ascospores uniseriate-overlapping, finally becoming subbiseriete above, ellipsoidal or broadly fusoid with rounded ends, hyaline or occasionally pale yellowish-orange, smooth, unconstricted, the lower cell often slightly longer and narrower, (9.0)11.0–15.1(16.0)×(4.0)4.7–6.1(7.0)μ, averaging 13.1×5.4μ.

Cultural characteristics.—On synthetic agar medium the aerial mycelium loose, sparse, radially appressed, becoming zonate, white to light buff (Ochraceous-Buff, Cinnamon); the surface mycelium well-developed, white to ochraceous (Light Ochraceous-Buff, Ochraceous-Buff, Cinnamon); on potato dextrose agar the sparse aerial mycelium more pinkish (Light Ochraceous-Salmon) fading to buff (Warm Buff); the surface darker (Ochraceous Tawny); upon either medium the subsurface coloration lighter (Pink Ochraceous or Light Ochraceous-Salmon) than the surface layer, or lacking; perithecial production rare; macroconidial columns lacking.

On steamed rice cultures agree in general with the darker cultures of *N. galligena,* with areas in the surface layer reddish-brown rather than brownish-olivaceous.

On the malachite medium, cultures agree with *N. galligena* in being tolerant of low and medium concentrations of dye, but agree with *N. coccinea* in not absorbing it; the range in index values for three cultures tested is 4.2 to 11.0; the average colony diameter on the control medium, 8.8 cm.

The conidial stage is a *Cylindrocarpon*, section *Ditissima* Wr. (31), intermediate between *C. mali* (Allesch.) Wr. and *C. candidum* (Lk.) Wr. Conidia variable in size, continuous to 6-septate, produced on bark either as a powdery waxy covering of the punctate, erumpent, yellowish to reddish-orange stromata that are up to 0.6 mm. in diameter, with the single-celled conidia predominating, or in smaller, chalk white to yellowish sporodochia of 0- to 6-, mostly 4- or 5-septate conidia; when continuous, elliptic-oblong or suballantoid, with rounded ends—when 3- to 6-septate, elongate, moderately curved (of 50 to 100μ radius), frequently somewhat narrower in the lower third, with apex rounded and walls of basal cell parabolic, the end slightly flattened; chlamydospores and pyriform conidia lacking; conidiophores simple or subverticillate, with continuous conidia developing in abundance about germinating ascospores, then later frequently agglutinated into false heads in young mycelia under moist cultural conditions. The following measurements for standard conidial types are based on conidial samples taken the fourth week from ascospore cultures of different origin grown on steam-sterilized yellowpoplar twigs at approximately 20° C.: 0-(3 cultures for 2 host species): (5.8)6.2–7.8(9.4)×1.8–2.8μ; 3-(3 cultures for 2 host species): 28–41×(3.8)4.0–5.0(6.0)μ; 5-(3 cultures for 2 host species): (44)52–62(68)×(4.0)4.5–5.5(6.0)μ.

The specimens, identified as this species and with few exceptions studied both culturally and biometrically, are from *Liriodendron tulipifera* L. (Connecticut, Ohio, West Virginia, Virginia, North Carolina, and Tennessee), *Magnolia fraseri* Walt. (West Virginia and Tennessee), and *M. tripetala* L. (West Virginia). The perithecial fruiting is usually abundant and regularly associated with stem or branch cankers. In cultures from fourteen field samples of different origin macroconidia were not obtained on ordinary laboratory media. Hepting, however, found them in old, drying cultures on a malt agar medium, identical with those that we have observed upon bark and in cultures of autoclaved twigs.

Nectria magnoliae is definitely intermediate between *N. galligena* and *N. coccinea*, differing from these species with respect to shape and size of macroconidia, size and profuse development of microconidia, progressive changes in coloration of perithecia, in ascospore size, cultural features on standard media, and in its capacity to produce cankers only on certain species of the Magnoliaceae. It differs from *N. galligena* in having smaller ascospores, curved macroconidia that are regularly shorter and fewer celled, smaller and relatively more slender microconidia, and a very limited host range. It differs from *N. coccinea* in having somewhat larger ascospores, more extreme variation in length of ascospore, less strongly curved and more slender macroconidia, smaller microconidia, parasitic habit, and in its limited host range. In as many aspects it differs from all varieties of *N. coccinea* and from *N. ditissima* Tul., as these species and varieties are

described by Wollenweber (35) and Richter (20); likewise, in so far as one can determine, it differs from *N. ditissima* Tul., in the sense of the Tulasnes (25). Considering morphologic features only, the *Cylindrocarpon* stage being excepted, upon final analysis this species could be interpreted as a variety of *N. galligena*, characterized by a definitely restricted host range, smaller ascospores, asci, and perithecia, the latter differing slightly in color and color change with age.

The pathogenicity of *Nectria magnoliae* has been tested in the field at Cherry Mountain, New Hampshire, in cross-inoculation experiments on hardwoods other than yellowpoplar in the 1934-series of inoculations reported by Spaulding, Grant, and Ayers (23), and on various hardwoods, including yellowpoplar, at Asheville, North Carolina.[15] With the eleven host species inoculated in New Hampshire, the results were negative except for paper birch, in which some cankering occurred on one of the two trees used but for which the results are inconclusive because of probable contamination by *N. galligena*.

In the North Carolina experiments, with respect to inoculations on *Acer saccharophorum*, *A. rubrum*, *Betula lenta*, *B. lutea*, *Fagus grandifolia*, *Juglans nigra*, *Liriodendron tulipifera*, and *Populus grandidentata*, *Nectria magnoliae* was noticeably less virulent than the various strains of *N. galligena* used. With respect to inoculations on *Quercus alba*, *Q. velutina*, and *Carya glabra*, both species were relatively inactive for the duration of the experiment. The lesions produced on *Liriodendron tulipifera* by a single strain of *Nectria magnoliae* isolated from that host and measured by cambial discoloration about the inoculation point, averaged 14 cm. in length, whereas those produced by 12 strains of *N. galligena*, isolated from 11 host species, averaged 19.7 cm. However, the lesions produced by these 12 strains on all other hosts averaged considerably greater, as much as 29.5 cm. in the case of a strain from *Juglans nigra*.

A culture of *N. magnoliae* isolated from *Magnolia fraseri* equaled in pathogenic activity the culture from *Liriodendron*.

The New Hampshire and North Carolina series are not comparable with respect to origin of strains used as inoculum, time of inoculation, and length of reaction period, although the same general technique was employed and trees were of approximately the same diameter.

In the anastomosing studies hyphae of different cultural origin were found to fuse with each other rather frequently and in certain instances, but to a lesser degree, with a few cultures of *Nectria galligena*. Fusions were not found in combinations with *N. coccinea*, *N. coccinea* var. *faginata* and *N. mammoidea*.

[15] The results here recorded for the two series of inoculations refer to unpublished data in Office Reports of the Division of Forest Pathology, by Dr. Perley Spaulding and Dr. G. H. Hepting, respectively.

Occasionally on *Liriodendron*, upon dead bark and wood of old cankers, especially those on dead stems, *N. sanguinea* and *N. episphaeria* appear in association with *N. magnoliae*. Undoubtedly they occur on the *Magnolia* species as well. *N. coryli* Fckl. likewise appears on fallen stems and branches of *Liriodendron*, but perhaps much less frequently since it was encountered in only a single instance in the present study (No. 67713, collected by G. H. Hepting, Bent Creek, North Carolina, June 1935). In so far as one can determine upon examination of specimens in herbaria, the *N. coccinea* Pers. ex Fr.—which is presumably the *N. ditissima* Tul. listed by Saccardo (Sylloge Fungorum **13,** 1898)—from smooth bark of *Magnolia fraseri* in West Virginia and from an undetermined species (probably *M. virginiana* L.) in New Jersey, agrees with *Nectria coccinea* from bark of *Acer saccharophorum* in New England, described herein. This species on *Magnolia* is exemplified in herbaria by the specimens of L. W. Nuttall and J. B. Ellis [*cf.* Ashcroft (1)]. We regard these specimens, at least No. 774 of J. B. Ellis, collected by L. W. Nuttall, Fayette County, W. Va., 1894, as being within the morphology shown by No. 380 of Desmaziere's Plantes Cryptog. de France, ed. 1 [*cf.* Weese (26), Ashcroft (1)].

3. Nectria mammoidea Phill. & Plowr.

Three collections of *Nectria* not found in immediate association with cankers are referred to *Nectria mammoidea* Phill. & Plowr., although they are not in complete agreement either among themselves or with either *N. mammoidea* or its variety *rubi* (Osterw.) Weese (Synonym: *Hypomyces rubi* (Osterw.) Wr.) as those forms are characterized culturally by Wollenweber (35, 37), the latter under its original name, *N. rubi* Osterw. These are of the following origin: No. 67790—on callus about basal fire scar, *Quercus velutina*, Pine Mountain, Georgia, August 6, 1935 (M. L. Lohman); No. 69610—on bark of dead, standing snag, *Quercus coccinea*, Oakland, Maryland, September 4, 1935 (R. C. Lorenz); No. 69675—on bark of stump, *Betula lutea* (2 years after tree with *N. galligena* cankers had been felled), Peru, Vermont, October 11, 1935 (T. J. Grant). Since this species may be confused with *N. galligena* because of variations in the external features of the perithecial stages of the two, and since our cultural studies were limited to but three specimens of what is essentially a species as complex and variable as *N. galligena*, certain diagnostic features in this "mammoidea-complex" are given in Table 2. Such features as the triplex wall of the coarsely verrucose perithecium, the flattened, strongly papillate, and usually dark-colored ostiolar region, ascospores becoming yellowish with unequal sides and conidia (*Cylindrocarpon janthothele* Wr.) of a size range and pattern characteristic of the mammoidea-complex, are common to the three numbered specimens, *N. mammoidea*, and its variety *rubi*.

The two specimens of southern origin, from *Quercus*, are in close agree-

TABLE 2. *Comparisons of American and European Nectrias of the "mammoidea-complex" exclusive of N. mammoidea var. rugulosa Weese and var. minor Reink.*

Diagnostic characteristics	American specimens			European specimens as described in the literature indicated	
	No. 67790 (On *Quercus velutina* in Georgia)	No. 69610 (On *Quercus coccinea* in Maryland)	No. 69675 (On *Betula lutea* in Vermont)	*N. mammoidea*[a] (On various hosts)	*N. mammoidea* var. *rubi* or *N. rubi*[a] (On various hosts)
Perithecia: Color and diameter (mm.)	Orange-red to reddish purple —0.4	Orange-red —0.4	Reddish-orange or orange —0.5	Red —0.51	Red —0.4
Ascospore size (μ) Mean	16.0×6.6	15.8×7.5	22.1×7.6	19.1×6.6	15.1×4.8
Normal	15.2–16.8×6.2–7.2	15–17×7–8	20–24×7.2–8.0	18–22×6–7[b]	15.9–18.6×4.6–5.2[c]
Extreme	14.2–18.6×5.8–7.4	14.8–17.6×7.0–8.4	19.4–24.2×7.2–8.6	14–25×6–9[d]	—
Ascospore wall	Smooth or punctate	Smooth or punctate	Punctate	Punctate	Punctate
Macroconidia	*Cylindrocarpon*	*Cylindrocarpon*	*Cylindrocarpon*	*C. janthothele* var. *majus* Wr.[e]	*C. janthothele* Wr.[f]
Septation	3–5– typically 3–	3–5– typically 3–	3–5– typically 3–	3–11– typically 4–5–	3–5–
Size (μ) Normal 3-)	38–54×5.2–6.7	48–56×6.0–7.0	34–43×5–6	48–60×5–6	48–57×5–8
5-)	50–56×6.3–6.8	58–63×6.2	42×5.4–6.0	58–82×5.0–6.5	56–60×5.7–8.5
Extreme 3-)	30–57×4.4–7.0	40–58×5.8–7.2	31–44×4.8–6.0	—	27–72×4–9[e]
5-)	44–63×5.4–7.8	(uniform)	(uniform)	—	40–80×5–11[g]
Coloration in culture	Cultures of two types—orange and violet-purple	Orange	Cream to orange with brownish orange sectors and droplets	Violet-purple	Violet-purple Also orange-brown in age with violet tufts and droplets[c]

[a] Features according to Wollenweber (35), unless otherwise indicated. [b] According to Ellis and Everhart, N. Am. Pyreno., 1892. [c] According to Osterwalder (16). [d] According to Petch (17). [e] According to Wollenweber (37). [f] See text for Osterwalder's measurements. [g] Compare Wollenweber (33).

ment with *N. mammoidea* var. *rubi* except for their broader ascospores and narrower conidia. Allowing for the personal element in measuring and for variations in size of conidia as produced under different cultural conditions, the differences to be noted in width of conidia are insignificant. Conidia in our cultures 67790 and 69610 are in closer agreement, however, with those observed by Osterwalder (16) who found them mostly 3-septate and of the size ranges 29–48×5.2–5.9(7.9)μ in some cultures, 50–57×6.6–7.9μ in others, and (42)53–61×6.6–7.9μ for 3- and 4-septate conidia on diseased roots of *Rubus*. With this variety the specimens do not agree in ascospore width and shape, for the spores are broadly fusoid as in *N. galligena*, rather than subfusoid as ordinarily described for *N. mammoidea* and the variety *rubi*. Ascospores of number 67790 were found to be relatively equally broad in perithecia produced on nutrient agar, with average measurements of 12.8×5.2μ in one culture and 12.6×5.3μ in another of different origin. If this fungus had not been observed in its perfect state in nature and had been obtained only in cultures from mycelia or conidia, it would

appear to be more closely allied with *N. mammoidea* var. *minor* Reinking (*Cylindrocarpon janthothele* Wr. var. *minus* Reinking) which Reinking (19) states differs from *Cylindrocarpon janthothele* Wr. (*Nectria mammoidea* var. *rubi*) chiefly in its conidia being narrower (3-septate: (5.3)5.7–7.2(7.8)μ in width—5-septate: (5.8)6.5–7.3(7.5)μ) and from *N. mammoidea* in its ascospores being smaller and conidia shorter. The relationship may not be real, inasmuch as Reinking obtained his *Nectria* from tropical American soils. Yet the perithecia of the Georgia specimen were on wound callus a few inches above the level of the soil and two tropical and subtropical bark-inhabiting Ascomycetes, namely, *Glonium clavisporum* Seaver and *Ostreion americanum* Duby, have been collected in abundance in the immediate vicinity.

The specimen from the bark of *Betula* (No. 69675) in New England differs from Wollenweber's conception of *N. mammoidea* in its shorter conidia with fewer septa and orange rather than violet-purple mycelia. However, of the three specimens studied this is typical *N. mammoidea* with respect to the features of the perfect stage. The ascospores are subfusoid, unequal-sided and minutely verrucose; the perithecial wall in vertical section shows the three layers, first discussed for the species by Weese (27), in this instance (1) an inner hyaline layer, 8–12μ thick, of narrow, vertical hyphae; (2) a central orange-red plectenchyma, 15–30μ thick, which becomes radial and darker upwardly, growing over the outer layer; (3) an outer layer, perhaps stromatic in origin, sometimes up to 40μ thick, of large, orange, globular or subglobose, loose-fitting cells that are responsible for the mealy appearance of unweathered mature perithecia. These layers are less pronounced in numbers 67790 and 69610; they are lacking in the perithecia of *N. galligena*, even in the case of the strongly papillate specimens that were mentioned in the consideration of that species.

The color of the culture in this species can be interpreted as a physiological strain difference. Our brief studies indicate, but do not prove, that possibly some ascospores from a perithecium produce orange mycelia and droplets, others violet-purple. In anastomosing studies, when purple mycelia of No. 67790 encountered orange mycelia of the same number and of 69610, the orange mycelia became purple within a single day. Likewise, when fragments of the purple colonies were placed upon the orange, the same change in color resulted. The material that colors these mycelia is upon the walls of the hyphae, especially the larger ones that bear sporodochia, as an amorphous secretion, smooth or in variably thickened masses just as Osterwalder (16) observed in his cultures of *N. mammoidea* var. *rubi* (Osterw.) Weese (*N. rubi* Osterw.).

The aerial mycelium is at first white, floccose-cottony, soon darkening and scarcely distinguishable from the surface layer. So-called orange or tan cultures are cinnamon or cinnamon-orange (Old Gold, Ochraceous

Tawny, Ochraceous Orange, Cinnamon Brown and Buckthorn Brown), the brighter colorations developing on the potato dextrose medium as compared with those on synthetic malt agar, with a brownish (Buckthorn Brown) discoloration of the medium. Purple cultures are bright (Light Perilla Purple to Deep Livid Purple) in the aerial mycelium but more brownish in the surface layer (Pale Brownish Drab, Light Seal Brown, Seal Brown, Fuscous), in general more or less mottled rather than uniformly colored.

On the malachite medium these cultures were tolerant of all concentrations of dye and showed a high degree of absorption. The index values range from 270 to 700. Colonies on the control medium averaged 4.7 cm. in diameter.

In the anastomosing studies hyphae of *Nectria mammoidea* of different cultural origin were found to fuse abundantly. Fusions were established with a few cultures of *Nectria galligena* but none in combinations with *N. coccinea*, *N. coccinea* var. *faginata*, and *N. magnoliae*.

4. Nectria coccinea Fr. *sensu* Wr.[16]

The American specimens of *Nectria* which we consider to be *Nectria coccinea* Pers. ex Fr. and most closely allied to European specimens of the species, as described by Richter (20), are from the bark of girdled or felled stems of *Acer saccharophorum* in Vermont (64086, 64155) and New Hampshire (70631). In these specimens scattered or densely clustered yellowish-red to orange-buff stromata break through the bark and develop one or more groups of closely colored perithecia which at first are concolorous with the stroma, later bright red and finally brownish-drab. By coalescence of groups on a common stroma (and similarly by coalescence of stromata) they frequently form clusters of 30 or more.

The perithecia are subconic, weakly papillate, and a little smaller than in *N. galligena* but with the wall size and structure noted for that species; the paraphyses are like those of *N. galligena* but less abundant; the asci

[16] For nearly a century specimens have been identified as *Nectria coccinea* Fr. which do not conform to the descriptions that Fries (7, p. 387, footnote) attached to that name. Furthermore, no fungus conforming to that description is known. In the further conservation of the name it appears to us that Wollenweber's first conception (34, pp. 304–305, plate 8, fig. H), to which he has applied it, is acceptable without presumptuous or confusing disposition of *Nectria ditissima* Tul., the position of which is discussed by Tulasne (25) and well reviewed by Ashcroft (1). In consideration of the features that must be employed in modern diagnoses of *Nectria* fungi, this conception is more readily adaptable than those which have been given subsequently by Wollenweber (35, 36, 37) and which are less in accord with various authors' conceptions. It should be expanded so as to comply with Wolenweber's (35, pp. 179, 201–202) subgeneric conception Coryneconnectria, and the section Willkommiotes as well, but not the extreme artificiality of the subsections Leiospora and Trachyspora established therein and used as the foundation for his more popular key (36, p. 555). This usage presupposes an understanding of *N. coccinea* as it is discussed or characterized by Weese (26, 29), Wollenweber (34, 35), Westerdijk and Van Luijk (32), Richter (20), Ashcroft (1), and Petch (17).

are more slender and the smooth-walled ascospores are uniformly obliquely uniseriate except for two or three at the apex at maturity. The ostiolar tissue, typically, is of weak development affording little contrast in color except during middle age when it is only slightly darker than the wall. Many of the younger arrested perithecia, possibly sterile and abortive, collapse from above, while the older, empty individuals collapse laterally but rather infrequently. Diagnostic features of asci, ascospores, and conidia are given in Table 1. The conidial stage is *Cylindrocarpon candidum* (Lk.) Wr.

Standard conidial types for cultures on autoclaved elm twigs at three weeks are of the following sizes: 0-): (4.0)4.7–11.8(13)×2.0–4.2(4.8)μ; 3-): (27)33–40(46)×(4.4)5.0–5.8(6.2)μ; 5-): 44–48×(5.2)5.6–6.2(7.0)μ.

It is primarily in the features of the macroconidial stage and coloration of the surface mycelia on standard media that this fungus differs from its close relative on beech.

Cultural characteristics.—On synthetic malt agar the aerial mycelium is whitish to yellowish (Buff-Yellow or Cream-Buff), subzonate and appressed but less noticeable in cultures that remain relatively light-colored; the surface layer in dark cultures is distinctly brownish (Raw Umber, Bister) and the subsurface coloration greenish-buff (Dark Olive-Buff); on potato dextrose agar the aerial mycelium as above but changing from whitish more quickly, especially in the darker cultures, becoming greenish-buff (Dark Olive-Buff) and concolorous with the subsurface layer of older cultures; the surface layers are brownish or reddish-brown (Chestnut Brown, Cinnamon Brown, Russet).

On steamed rice the aerial mycelium is white, velvety, and conspicuous, much as in *N. galligena;* the surface mycelium in light cultures is whitish, becoming lemon-yellow (Citron Yellow, Pale Lemon Yellow, Lemon Yellow) and remaining so for several weeks—in dark cultures *soon* yellowish or yellowish-orange (Cadmium Yellow, Mars Yellow, Xanthine Orange), then dull grayish-brown (Brownish Olive, Buffy Brown).

On the malachite medium the mycelia are only tolerant of low concentrations of dye, show no absorption, and are of the range 1.5 to 2.8 in index values. Colonies on the control medium averaged 9.1 cm. in diameter.

The dark brownish-olive and reddish-brown stromata in the surface layer of dark cultures, eventually with macroconidial columns and in certain cultures perithecia, afford a reliable, macroscopic separation between this species and the darkest cultural types of *Nectria galligena.* In cultural characteristics these specimens are in general agreement with Richter's (20) *N. coccinea* and the variety *minor* Wr.

Ascospores in these specimens, however, are slightly broader in relation to their length and also somewhat longer than in European specimens. The ascospore means for the above-numbered specimens are 12.8×6.0,

13.0×5.6, and 12.6×5.3μ, respectively. Richter's specimens of European origin, from beech, average 11.1×4.5μ, with a normal range of 9.0–13 ×4–5μ. In the case of perithecia produced on nutrient agar, samples from seven cultures of different origin in our number 64086 gave mean ascospore lengths ranging from 12.4 to 13.9μ and mean widths from 4.8 to 5.5μ, the mean size for combined samples with a total of 215 ascospores being 12.7 ×5.3μ. This feature, then, for field material and pure cultures of the fungus, is in closer agreement with Wollenweber's first report of ascospores being normally 10–15×4.75–5.25μ.

The fungus cannot differ greatly from Richter's *N. coccinea* var. *minor* Wr., of *Acer* and *Laburnum*.

In field inoculations at Liberty, Maine, a culture of recent origin produced no bark lesions on 8 large beeches infested with the scale insect. A different isolate also was inactive in the above-mentioned inoculations at Cherry Mountain, New Hampshire, on healthy beech, apple, aspen, white ash, pin cherry, red maple, and sugar maple but presumably formed the questionable, weak lesions on paper and yellow birch, mountain maple and striped maple. The inactivity noted is attributed to relative virulence of the particular cultures since in both series definite cankering resulted in the case of inoculations with cultures of *Nectria galligena*.

In the anastomosing studies hyphae of different cultural origin were found to fuse freely and in certain instances to an equal degree with both light- and dark-colored cultural types of *N. coccinea* var. *faginata*. Fusions were not found in cultural combinations with *N. galligena*, *N. magnoliae*, and *N. mammoidea*.

5. **Nectria coccinea** var. **faginata** Lohman, Watson, and Ayers, var. nov.

Perithecia ovoidea vel subglobosa, coccinea, dein paulo griseola purpureo-coccinea, 240–380×200–315μ, typice gregaria, raro in ligno et cortice sparsa, 7–15 vel 20–35μ in stromatibus corticis erumpentibus rubicundulo-aurantiacis et circubariter aggregatis; asci cylindrico-clavati, primo truncati, 63–84×7–12μ, moniliformiter paraphysati; ascosporae ultimo inordinato subbiseriatae, glabrae vel subtiliter punctatae, ellipsoideae vel crassi-ellipsoideae, 12.3×5.9, plerumque 11–13.6×5.2–5.7 (8–18×4–7)μ; mycelia culturarum primo albida dein castanea, conidifera (*Cylindrocarpon*), aeria floccosa, plus minusve zonata, peritheciis raro praedita; microconidia varie elongato-ellipsoidea, 8 14.8×2.2–3.8μ, libera vel in capitulis falsis vel sporodochiis tuberculariibus disposita; macroconidia elongato-subcylindracea, arcuata, 5(1–8)-septata, 5-: circa 58–100 ×5.5–6.5(49–114×5.0–7.0)μ, in sporodochiis extremum columnis flavis 3–12 mm. longis; chlamydosporae nullae.

Hab. in cortice destructo truncorum vivorum *Fagi grandifoliae*.

Obs. Fungus a *Nectria coccinea* Fr. *sensu* Wr. eiusque var. *longiconia* Wr. differt praecise ascosporis crassioribus, macroconidiis majoribus et charactere culturarum et habitus.

Type specimen: No. 63940. On *Fagus grandifolia*, bark of living tree infested with beech scale insect; Meddybemps, Maine. T. T. Ayers. Oct. 4, 1933—Mycological Collections, Bureau of Plant Industry. (Ex-type: Farlow Herbarium, Harvard University; The New York Botanical Garden; University Herbarium, University of Michigan.)

The following para-type specimens, all taken on *Fagus grandifolia*, accompany the type: No. 53886. Liberty, Maine. R. P. Marshall. May 4, 1933—No. 53887. Perry, Maine. K. Aldrich and H. McKenzie. May 4, 1933—No. 53889. Mariaville, Maine. K. Aldrich and M. McKenzie. May, 1933—No. 63942. Perry, Maine. T. T. Ayers. Oct. 6, 1933.

Perithecia superficial upon orange or reddish-orange stromata erumpent through bark in irregular lines or in circular areas up to 3 cm. diam., ovoid or at maturity subglobose, in clusters of 7–15 upon a common stroma and by coalescence as many as 20–35 or more, papillate-ostiolate, sometimes collapsing from above when immature and from the side when matured, reddish-orange or bright red, sometimes purplish at the base, finally reddish or brownish-drab, the ostiolar tissue weakly developed but definite and frequently slightly darker than the lateral wall, normally 240–380 $\times$200–315μ, walls parenchymatic, 15–30μ thick, weakly radially prosenchymatic above, the colored cells below typically oblong or elongate-angular in vertical sections; asci 8-spored cylindric-clavate, broadly truncate above, then subtruncate-rounded 63–84$\times$7–12μ, short stipitate, tufted and paraphysate; paraphyses moniliform, tapering simple or branched, thin-walled with basal cells swollen, persistent but not abundant; ascospores uniseriate-overlapping, finally irregularly subbiseriate above, ellipsoidal or broadly ellipsoidal, smooth or minutely punctate, sometimes slightly constricted, hyaline, measuring (8.0)11.0–13.6(18.0) $\times$(4.0)5.2–5.7(7.0)μ, averaging 12.35$\times$5.96μ.

Cultural characteristics.—On synthetic agar medium the aerial mycelium floccose, broadly zonate or azonate, whitish, then brown (Tawny); colorations of the surface and subsurface equal to *Nectria coccinea* except for more reddish tints (Chestnut and Auburn) in the stromatic layer, particularly in the erumpent areas and in the case of so-called darker cultures; on potato dextrose agar more yellowish-brown (Tawny) in the aerial mycelium and rather uniformly reddish-brown (Chestnut) in the surface layer, persisting thus in light cultures but becoming deep reddish-brown (Mahogany Red) in the more frequent dark culture-type; perithecial production occasional; macroconidial columns frequent, long, cream or whitish, in age splitting and recurved.

On steamed rice aerial mycelium, sparse, whitish but soon yellowish;

surface mycelium stromatic, either yellowish-orange (Cadmium Yellow) changing to orange-brown (Mars Yellow), or at first mottled yellowish-brown and orange-brown (Xanthine Orange) and then changing to deeper brown (Raw Sienna).

On the malachite medium the mycelia are only tolerant of low concentrations of dye, show no absorption, and are of the range 1.6 to 2.3 in index values. Colonies on the control medium averaged 7.5 cm. in diameter.

The conidial stage is a *Cylindrocarpon*, section *Ditissima* Wr., near *C. candidum* var. *majus* Wr. (status conid. *Nectriae coccineae* var. *longiconiae* Wr. (37, p. 158, 159). Conidia variable, continuous to 8-septate, on cream-colored sporodochial stromata erumpent through the bark and in culture in the case of microconidia, in false heads on simple or branched conidiophores and, in the case of macroconidia, in scattered, simple sporodochia, slimy rounded droplets, or at last in curved, cylindric, cream to yellowish-orange columns 3–12 mm. in length; when continuous, elongate ellipsoidal, sometimes unequal-sided or suballantoid, 8–14.8×2.2–3.8μ; when 3- to 8-septate elongate subcylindric, moderately curved, with ends elliptic to obtusely rounded in outline. The following macroconidial measurements for standard conidial types indicated are for samples taken from ascospore cultures, held at approximately 20° C., on various media in the fourth week: 3-(7 random cultures on each of the standard media): (35)42–54(60)×(5.8)6.2–6.9(7.2)μ; 5-(7 random cultures on each of the standard media): (49)58–82(95)×(6.6)6.8–7.6(8.2)μ; 5-(1 random typical dark culture on oatmeal agar): (84)88–100(114)×(5.0)5.5–6.5μ.

The following measurements are of interest in comparison: 5-(1 random field sample): (69)74–86(90)×(5.5)6.0–6.5(7.0)μ; 5-(7 cultures, as reported by Ehrlich (6)): (50)67–93(115)×4.6–6.0μ; 5-(*N. coccinea* var. *longiconia*—Wollenweber (37)): 51–75×5–6μ; 5-(*N. coccinea* var. *longiconia*—Richter (20)): 50–82×5–7μ.

This variety is known from the Canadian Maritime Provinces, Maine, and New Hampshire on the bark of *Fagus grandifolia*, occurring presumably only occasionally on healthy bark, but usually in abundance once infections are established on bark infested by the beech scale insect.

Whether this *Nectria* is native to the Canadian Maritime Provinces and the eastern States and has been able to increase in an alarming degree on American beech under changing ecological conditions, or whether it has been introduced from Europe or elsewhere remains highly problematical.[17] Its occasional occurrence on *Acer*, *Betula*, *Carya*, *Juglans*, and *Quercus* may be expected in view of the host ranges of *Nectria* species in greneal—although as in this instance some varieties at the present time are known only for a single host genus. If these fungi are limited to particular phylogenetic sequences of their hosts, this particular variety eventually may be

[17] Of further interest in the problem of host relationships is a recent paper by T. T. Ayers (2).

found in some temperate region on *Aesculus*, *Ilex*, *Rhamnus*, or *Rhus*, if not on the hosts previously mentioned.

The variety differs from *Nectria coccinea* primarily in its larger conidia, relatively broader ascospores, cultural characteristics and nutritive relationships in the forest. In similar respects it differs from *N. coccinea* var. *longiconia*, with which variety, as Ehrlich (6) likewise concluded, it appears to be most closely related. Wollenweber (37) recognized his variety on bare wood and bark of stems and branches of species of *Acer*, *Fagus*, and *Fraxinus* in Europe, and *Juglans* from Oregon, U. S. A.

In the series of field inoculations noted in the foregoing treatment of *Nectria coccinea*, 5 cultures of different origin were used upon 16 large, scale-infested beeches in the Liberty area and 3 cultures of different origin on the 11 host species in the Cherry Mountain area. In these inoculations certain cultures proved to be consistently nonpathogenic to beech with healthy or scale-infested bark; others proved to be consistently pathogenic (as judged by circular bark lesions) to the bark of insect-infested beech with questionable injury to the true cambium and nonpathogenic (as judged by bark lesions and alterations of the true cambium) on healthy beech and other host species.

In the anastomosing studies hyphae of this variety of *Nectria coccinea* of different cultural origin were found to fuse freely; in certain combinations with *N. coccinea* to an equal degree; and in one of 15 combinations with cultures of *N. galligena*, to a lesser degree. In combinations with *N. mammoidea* and *N. magnoliae* fusions could not be found.

6. Nectria cinnabarina, N. coryli, N. episphaeria and N. sanguinea

As mentioned in the discussion of *Nectria magnoliae*, other species of *Nectria* that are commonly reported as saprophytes on decaying wood or on the bark of dead twigs and stems occasionally may occur within or adjacent to the cankered areas upon which the fruiting of *N. galligena* and *N. magnoliae* has continued, more particularly upon dead twigs and stems. In the present study the following four species have been encountered, brief diagnoses of which, largely as adopted from the taxonomic treatment by Seaver (22), are given for ready comparison.

Nectria cinnabarina (*Creonectria cinnabarina* L. ex Seaver) is recognized upon bark by the conspicuous, cinnabar or purplish-red conidial stromata (*Tubercularia*), typically upon or about which, later, the similarly colored, roughened perithecia appear in dense clusters. The conidial stromata average 1.5 mm. in diameter and in height; the perithecial clusters, a little larger. Conidia are numerous, hyaline, continuous, 4–6×2μ; perithecia, 375–400μ in diameter, frequently brownish or grayish, when weathered; paraphyses, branched, delicate, hyphalike, septate, of uniform

diameter throughout; ascospores elongate-elliptic, somewhat curved and with rounded ends, 12–20×4–6μ, tending to remain biseriate.

In our cultures the mycelia on nutrient agar are sordid white, smooth-surfaced, usually conidia-bearing, and of more rapid growth than those of *Nectria galligena*.

NECTRIA CORYLI fruits upon bark of twigs. The stromata are erumpent but comparatively inconspicuous and the perithecial clusters resemble those of *N. coccinea* and *N. magnoliae* until weathered, when they are darker. The fungus is recognized most readily by the numerous conidia accompanying ascospores within the ascus. Ascospores are hyaline, elongate-elliptic with apiculate appendages, and measure 10–15×3μ; paraphyses resemble those of *N. cinnabarina*. Macroconidia are unknown.

In our cultures mycelia on nutrient agar are sordid white, smoothish, and produce conspicuous bundles of needle-shaped, golden crystals.

NECTRIA EPISPHAERIA (*Sphaeria episphaeria* Tode) is found fruiting upon the stromata or perithecia of sphaeriaceous fungi. At times, as for example in the case of occasional cankers produced by *N. galligena* on *Juglans* and the greatly elongated, bark-covered cankers of *Sassafras*, in connection with which *N. galligena* is unknown, it appears to be fruiting directly upon the host plant tissue and is probably fungicole. This species is recognized by its minute, scattered or loosely gregarious, blood-red to pinkish-red perithecia, 150–250μ in diameter, and the small, oblong or broadly fusoid ascospores, 9–12×4–6μ. The conidial stage is a *Fusarium* with conidia few-celled, slender, moderately to strongly curved, yellowish to salmon in mass. Wollenweber's (38) measurements indicate a smaller ascospore with average size 8.3×3.5μ, the 3-septate conidia of which average 42×2.7μ and conform to *Fusarium aquaeductum* (Radlk. & Rab. *pr. p.*) Lagh. var. *medium* Wr.

NECTRIA SANGUINEA (*Sphaeria sanguinea* Sibth. ex Fr.) fruits upon exposed or weathered wood. Specimens thus identified are recognized, according to Seaver (22), largely by their habitat, scattered perithecia, and subelliptical or narrowly fusoid, granular ascospores. The perithecia are recorded as averaging a little larger than those of *N. episphaeria;* the ascospores as measuring 10–12×4–5μ.

Weese (28) considers *Nectria episphaeria* and *N. viticola* Berk. & Curt. synonyms of *N. sanguinea*. According to Weese many specimens of exsiccati under these names are *N. coccinea*, which includes, in Weese's usage, *N. ditissima*. The specimen distributed as *N. sanguinea* by Wilson and Seaver, however, he considers to be properly named. He places *N. pithoides* Ell. & Ev. in the synonymy of *N. applanata* Fr., which name, in his opinion, designates a distinct but closely related species.

Petch (17) lists *N. episphaeria* as a synonym of *Dialonectria sanguinea* (Sibth. ex Fr.) Cke., thus accepting *Sphaeria sanguinea* in a broad sense, as does Weese.

Of the above-mentioned species only two cultures of *Nectria cinnabarina*, of different origin, were used in the field inoculations.[18] These cultures represented apparently parasitic strains of the fungus associated with the die-back of twigs of European beech and Japanese maple in Massachusetts, following winter injury. In the inoculations, one strain (maple) was entirely inactive; the other, generally inactive, although a few doubtfully significant bark lesions were produced by it on mountain maple, sugar maple, paper birch, and yellow birch.

SUMMARY AND CONCLUSIONS

Nectria fungi found in association with stem diseases of hardwood species in the New England and Appalachian forest areas were grouped according to features now commonly recognized as important in the systematic treatment of these fungi. The specimen groups were then compared biometrically in regard to ascospore size and representative cultural types were examined with respect to differential growth in response to malachite green in a special nutrient agar medium and with respect to degrees of anastomosing between hyphae of different cultural origin in paired combinations on a standard medium, the two latter methods of verifying either species relationships, or the usefulness of simple analytical groups, not heretofore having been employed in the study of *Nectria* fungi.

Such species as *Nectria cinnabarina*, *N. coryli*, *N. episphaeria* and *N. sanguinea* were encountered one or more times. This paper, however, is concerned with the following species: *N. coccinea* Fr. *sensu* Wr., as found on bark of *Acer saccharophorum* in New England; *N. coccinea* var. *faginata*, var. nov., from weak and in most instances scale-infested, diseased bark of *Fagus grandifolia* in New England and the Canadian Maritime Provinces; *N. galligena* from bark, callus tissue, and recently exposed sapwood, particularly in association with cankers and on bud-scale scars of various hosts throughout the eastern States; *N. magnoliae*, sp. nov., from bark, callus tissue, and recently exposed sapwood of *Liriodendron* and species of *Magnolia* especially in association with cankers, from Connecticut to Ohio and southward through the Appalachian area; and with three rather distinct variations of *N. mammoidea* Phill. & Plowr. as found on dead *Betula* in Vermont, on dead *Quercus* in Maryland, and on living *Quercus* in Georgia, with little indication of parasitism. For these Nectrias morphological and cultural characteristics are described, host relationships are discussed, and important diagnostic features are tabulated.

Nectria galligena of American beech and other hosts is in agreement with European Nectrias referred to that species or its variety, var. *major*, or to *N. ditissima* sensu Wr. and certain of its varieties. The saprophytic *Nectria coccinea* of sugar maple is in close agreement with that species on European

[18] Reference is to inoculations at Cherry Mountain, New Hampshire and Cobalt, Connecticut (see footnote 5).

beech in Europe, on *Magnolia* in the eastern States as judged from early herbarium specimens, and perhaps identical with that species on various hosts in Oregon in view of certain reports in the literature.

Considerable variability is shown for *N. mammoidea*, which remains unstudied as to pathogenicity and which in the few previous records for the eastern States probably has been confused with *N. galligena*.

The recognition of those above-mentioned groups of Nectrias on the basis of any single morphological or cultural characteristic is of limited reliability. Form and mean size of ascospore (the mean of 25 free spores from a mixture of ascospores from several perithecia), shape of microconidia and macroconidia, and progressive colorations and mycelial habit on standard culture media (synthetic malt and potato dextrose agar media, and steamed rice) are the most reliable features. Size, coloration and arrangement of perithecia, nature of the ostiolar tissue, shape and size of ascus, punctation of ascospore wall, and size and septation of macroconidia are of secondary value.

Both pathogenic and nonpathogenic cultural strains are recognized for *N. galligena* and *N. coccinea* var. *faginata* and no single morphological feature or cultural characteristic was found to serve as a guide to the probable virulence of a given specimen or culture of either.

Nectria galligena cannot be considered strictly a canker *Nectria* of Rosaceous hosts. *N. galligena* var. *major* can no longer be restricted to the genus *Fraxinus*.

It is to be noted that *N. coccinea* var. *faginata*, which is commonly associated with the scale infestation and dying of American beech, has not been observed on *Acer*, *Betula*, *Carya*, *Juglans*, and *Quercus* and that it is not recognized for reasons of geographical distribution or host specificity, but rather, because it does not conform to recent descriptions of European specimens of *N. coccinea* or varieties of that species.

The gross cultural characteristics of these Nectrias are useful either for the tentative determination of cultures or specimens, when considered alone, or for the critical identification of specimens, when observed in conjunction with size and shape of ascospores and conidia. There is appended a brief outline of these features as they were observed on three of the nutrient media employed.

I. Slant cultures prepared by single point inoculum on either synthetic-malt or potato-dextrose agar media (indicated in the following synopsis as S.M. and P.D., respectively).

A. Aerial mycelium typically floccose-cottony (in No. 1 sometimes cottony on P.D.); that of the surface layer stromatic (except in No. 3); the *darkest colorations* of the mycelia of the following categories, each with its respective coloration of the subsurface layer.

a) S.M.: Aerial, light cinnamon or buff—Surface, chalk to brownish—Subsurface, concolorous, or lighter, or darker.

P.D.: Aerial, light cinnamon-brown—Surface, rich brown—Subsurface, concolorous, or lighter, or darker..... No. 1. *N. galligena.*

b) S.M.: Aerial, brown—Surface, chestnut to auburn (usually mottled)—Subsurface, greenish-buff.
P.D.: Aerial, yellowish-brown—Surface, chestnut to mahogany (usually unicolorous)—Subsurface, greenish-buff.....No. 5. *N. coccinea* var. *faginata.*

c) S.M.: Aerial, cinnamon-orange, or purple—Surface, brownish-drab or fuscous (usually mottled)—Subsurface, brownish.
P.D.: Aerial, cinnamon, or bright purple—Surface, ochraceous-orange or bright purple (usually mottled)—Subsurface, brownish.....No. 3. *N. mammoidea.*

B. Aerial mycelium inconspicuous (greatly appressed) or sparse, loose and noticeably radially appressed; that of the surface layer very weakly stromatic; the *darkest* colorations of the mycelia of the following categories, each with its respective coloration of the subsurface layer.

a) S.M.: Aerial, light buff—Surface, ochraceous—Subsurface, lighter, or medium unchanged.
P.D.: Aerial, pinkish, then buff—Surface, ochraceous-tawny—Subsurface, lighter, or medium unchanged.....No. 2. *N. magnoliae.*

b) S.M.: Aerial, yellowish—Surface, brownish or reddish-brown but as frequently uncolored—Subsurface, greenish-buff (in "dark" cultures) or medium unchanged (in "light" cultures).
P.D.: Aerial, greenish-buff—Surface, as on S.M.—Subsurface, as on S.M.....
.....No. 4. *N. coccinea.*

II. Diffuse cultures on steamed rice inoculated with conidia and mycelial fragments in suspensions.[19]

A. Aerial mycelium conspicuous, velvety, white; that of the surface layer dense, soon colored.
a. Cultures yellowish or pale greenish-buff, sometimes becoming brownish, olivaceous or with areas of rich brown.....No. 1. *N. galligena.*
b. Cultures as in *N. galligena* except the darkest areas typically reddish-brown.....
.....No. 2. *N. magnoliae.*
c. Cultures either soon lemon-yellow and remaining so or at first yellowish-orange and becoming dull grayish-brown.....No. 4. *N. coccinea.*

B. Aerial mycelium sparse and soon scarcely distinguishable from the stromatic surface layer.
a. Cultures either yellowish-orange, becoming orange-brown, or soon orange-brown, becoming deep rich brown.....No. 5. *N. coccinea* var. *faginata.*

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[19] *Nectria mammoidea* was not grown on this medium.

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Contributions to the Life History, Morphology and Phylogeny of Widdringtonia cupressoides[1]

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INTRODUCTION

A fairly complete life history of *Widdringtonia cupressoides* (L.) Endl. has been worked out by earlier authors, notably Saxton (1909, 1910a, 1934). Morris (1909–1910), Hill and de Fraine (1908) and Masters (1895, 1905) contributed several details of lesser importance. But there remain several gaps in our knowledge of the species, most of which the present author is able to fill now.

The genus *Widdringtonia*, Endl., Gen. Pl., Suppl. II: 25, 1842, is composed of at least seven well defined species of evergreen trees and shrubs, occurring in South Africa and Madagascar (Chalk, Davy and Desch, 1932). The genus is closely related to the genera *Callitris*, *Actinostrobus*, *Tetraclinis* and *Fitzroya*. The species *Widdringtonia cupressoides* is a shrub 6 to 12 feet high, occurring at an altitude of 2000 feet or higher, in the Table Mountain Range, eastward, and along the Amatolas and Transkei of Cape Province, South Africa.

The synonym of the genus *Widdringtonia* is as follows:

Pachylepsis, Brongn., Ann. Sci. Nat. **30**: 189, 1833, non Lessing.
Parolinia, Endl., Gen. Pl., Suppl., I: 1372, 1840.
Widdringtonia, Endl., Gen. Pl., Suppl. II: 25, 1842.
Widdringtonia, Endl., Syn. Conif., pp. 31, 1847.

Species of *Widdringtonia* have been repeatedly placed in the genus *Callitris;* see Bolus and Wolley-Dod (1903), Bentham and Hooker (1842), Eichler (1889), Jackson (1895), and Marloth (1905). The genus, however, was established and properly described by Endlicher (1842, 1847), and since then has received authoritative recognition by Maiden (1904), Masters (1895, 1905), Pilger (1926), Rendle (1930), Sim (1907), and Saxton (1909).

The family Cupressaceae of the Coniferales is sub-divided in various ways by different authors. According to Saxton (1910b), however, the Cupressaceae should be divided into at least two sub-families: the Callitroideae, containing the genera *Actinostrobus*, *Callitris* and *Widdringtonia*, and the Cupressoideae, containing the remaining genera of the family. *Tetraclinis* and *Fitzroya* have affinities with both groups; but they should probably be considered as belonging to the Cupressoideae.

[1] I wish to thank Professor John T. Buchholz of the University of Illinois for his direction of this investigation, Dr. James M. Schopf of the State Geological Survey of Illinois for the use of photographic equipment, and Mr. Eric Walther of the Golden Gate Park, San Francisco, California, for collections of material.

MATERIALS AND METHODS

The author investigated several details of the life history of *Widdringtonia cupressoides* as well as a few details of the gross morphology of the reproductive structures. The gametophytogenesis and embryogeny of this species represent a continuous process with no intervening dormant periods from the appearance of cones to the final development of the embryo; and, apparently, the ovules of different cones borne in the same cluster may be at several different stages of development on the same date. Table 1 depicts the dates of collection and the stages of development of the ovules at different collection dates.

TABLE 1

Collection	Killed and Fixed	Stage of Development
Aug. 16, 1940	Aug. 16, 1940	Pre-fertilization of very young embryos
Aug. 24, 1940	Aug. 24, 1940	Young embryos
Sept. 3, 1940	Sept. 3, 1940	All stages of embryo development
Sept. 10, 1940	Sept. 10, 1940	
Oct. 12, 1940	Oct. 17, 1940	Young and nearly mature embryos
Dec. 3, 1930	Dec. 9, 1940	All stages of development

All collections were made from a specimen growing in the "Golden Gate Park," San Francisco, California. Some of the collections were killed and fixed on the same day; in the last two collections, the embryos were dissected out of the ovules before killing and fixing.

In all cases, a solution consisting of 5% commercial formalin and 2.5% acetic acid in 50% ethyl alcohol was used as a killing and fixing solution. Ovules that were dissected after killing and fixing were dissected in 50% ethyl alcohol; ovules dissected before killing and fixing were dissected in a 15% sucrose solution, which is considerably below an isotonic solution, but of sufficient osmotic concentration to prevent, during dissection, the rupture of cells composing the embryo.

Serial sections were made of all stages, and more than 150 whole-mounts of embryos were made from all collections, except the first. For serial sections, the ovules with the integuments removed were run up through an alcohol-xylol series and embedded in paraffin. The integument is practically impermeable to all solutions and to paraffin; and the nucellus, likewise, has a very poor permeability. A butyl-alcohol (butanol) series was first used, but the penetration of tissues was not successful. By using xylol as the paraffin solvent and by increasing the time for infiltration to 72 hours at 51° C., and the time in paraffin up to 96 hours, about 75% good infiltration was attained. Serial sections were stained with Heidenhain's haematoxylin and counterstained with Orange G.

The whole embryos were stained in phloxine and mounted in diaphane. The technique of dissection, dehydration and mounting is adequately described by Buchholz (1938).

GROSS MORPHOLOGY

A rather complete description of the genus and species, including general morphological and anatomical features, may be found in Chalk, Davy and Desch (1932) as well as in such sources as Pilger (1926), Rendle (1930) and Masters (1895, 1905).

The ensuing description will deal mostly with the reproductive parts, but a few brief remarks on the foliage of the species may be of interest. In general, the foliage resembles that of *Cupressus* or *Juniperus*. The leaves on the juvenile plants and on the long-shoots of the adult plants are linear, flat, long-pointed and spirally arranged. The first leaves above the cotyledons, however, are in whorls (Florin, 1930; Saxton, 1909). The leaves on the adult plant, with the exception of the long-shoots, are scale-like, adpressed and arranged in alternating, opposite pairs. A representation of the mature leaves may be seen at the base of the male cone, fig. 1.

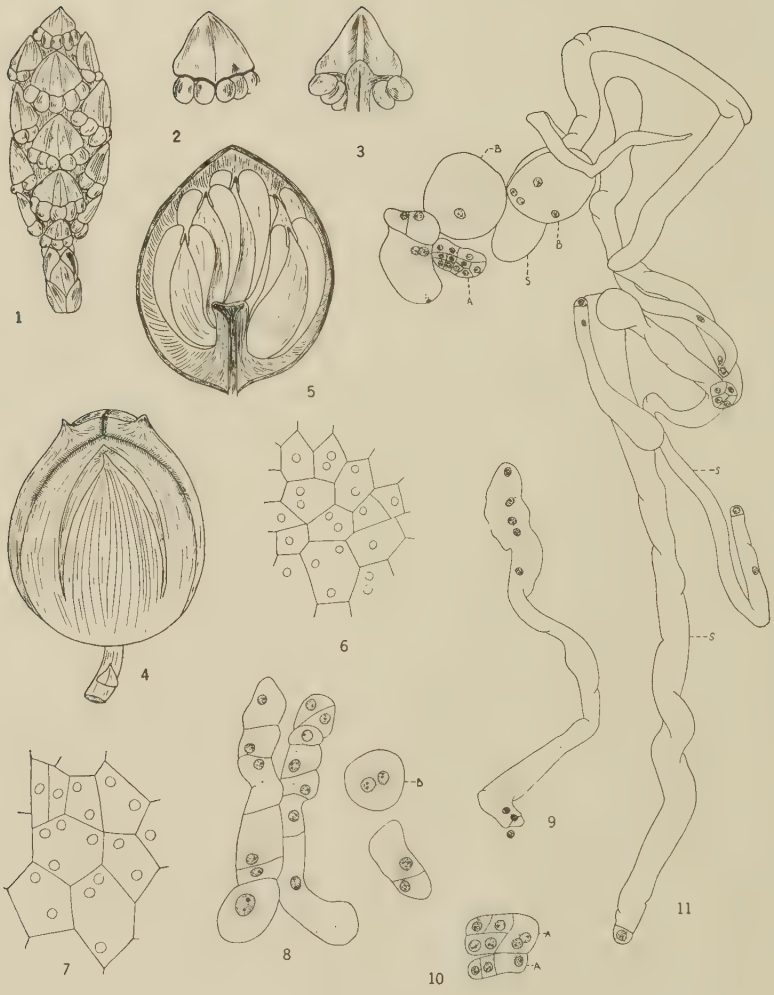
The male cone.—The cones of the genus *Widdringtonia* are unisexual and the species are monoecious. The male cone is very small and rarely attains a length of over 4 millimeters. The cone is solitary, sessile and usually terminates a short-shoot. It is composed of microsporophylls arranged in decussate pairs (fig. 1).

The microsporophylls are nearly erect, somewhat carinate with the convex face outward, and each bears three to five microsporangia on the lower portion (fig. 2). It can hardly be said that the microsporangia are borne on the abaxial side of the scale, as would seem typical for conifers; rather, they seem to be attached in a longitudinal row at the very base of the scale; and, if anything, they are attached to the adaxial side (fig. 3). The microsporangia, at maturity, project downward from the scale as elongated, ovoid sacs (fig. 1). Figure 2 of Saxton (1909), however, is a drawing of a longitudinal section of the male cone in which the microsporangia appear as attached to the abaxial side of the microsporophyll. The only explanation of this discrepancy is that Saxton and the present author have studied the cones at different stages of ontogeny.

The male cones mature at about the same time that the female cones are open with their scales widely spreading, indicating that pollination takes place at this time.

The ovulate cone.—The female cones are axillary on short stalks and are often grouped together in large numbers. The cone is composed of two decussate pairs of scales, two of which have squared distal tips which contact each other distally, while the other two are shorter, have pointed distal tips, and do not contact each other (fig. 4).

According to Saxton (1909), each scale of the mature cone bears five to eight ovules apparently on the proximal half of the adaxial surface close to the central ridge. The ovules in a young cone, however, appear to be evenly distributed over the broadened end of the axis. On the basis of



EXPLANATION OF PLATES

Figures 1–20, inclusive, are camera lucida drawings; figures 21–26, inclusive, are photomicrographs taken at various magnifications as indicated. In all figures: 'A' represents abnormal, proembryo-like embryonic structures; 'B' represents an embryonic unit which enlarged rather than elongated (spherical cell); 'e' represents a single embryonal cell of the secondary suspensor; and 'S' represents the primary suspensor.

FIG. 1. The mature male cone showing the arrangement of the microsporophylls. ×12.

FIG. 2. A single microsporophyll with five microsporangia as seen from the abaxial side. ×20.

FIG. 3. A single microsporophyll from the adaxial side showing the attachment of the microsporangia. ×20.

FIG. 4. A single ovulate cone showing the arrangement of the scales and general characteristics. ×3.

FIG. 5. A single scale of the ovulate cone, demonstrating the shape and attachment of the ovules as seen from the adaxial surface. ×3.

observations, the author would tend to support the view that the ovules are in reality attached to the axis as they arise ontogenetically from the axis and not from the scales. It seems better to accept the ontogenetical evidence in this respect, as did Hagerup (1933) in his brilliant research on the morphology of coniferous ovulate cones, and consider the mature attachment as only apparent and secondarily developed by the fusion of the bases of the cone scales with each other and with the axis. In the author's opinion, even in the mature cones, the ovules are attached to the axis and not to the fused scale bases (fig. 5).

The mature female cones are ovoid to globose, erect, woody and persist for some time after shedding the seeds (fig. 4). According to Saxton (1910a), each megasporophyll possesses a large number of vascular strands and resin canals; and at the distal end of the sporophyll, the resin canals are regularly disposed around the periphery, and within each is a vascular bundle. The scales of the mature cone are woody, tough, very resinous, convex, brown to greenish-brown and lack the tubercles of the other species of *Widdringtonia*. Each scale bears an umbo or short projection near the distal end of the abaxial surface. Saxton rejects the possibility that the umbo is the reduced bract.

The youngest ovulate cone that has been seen was about 3 to 4 millimeters in diameter. At this stage, the two decussate pairs of scales were widely spreading. The closed mature cone has a longitudinal diameter of about 1.7 centimeters and a transverse diameter of about 1.9 centimeters.

The author dissected one very compact cluster of twenty-two cones. All were borne on short axes which in turn were attached to three main branches whose total length scarcely reached 6 centimeters. Thirteen of these cones were nearly mature, while nine were still immature, small and green. The cones nearer the main branches, at the base of a given cluster, tend to be more mature than those more distal.

The ovule.—The ovule is often curved, always erect, and bears two rather thick lateral wings, one of which tends to be more strongly developed than the other (fig. 5). The integument is unusually thick and almost impermeable to fixing solutions, alcohols and paraffin. There is a long tubular

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FIGS. 6 and 7. Semi-diagrammatic drawings of the mature megagametophytic tissue composed of uninucleated, binucleated, and multinucleated cells. ×330.

FIG. 8. Abnormal embryonic structures found in the region of fertilized archegonia. Explanation in the text. ×225.

FIG. 9. An abnormally elongated embryonic unit containing eight nuclei. ×130.

FIG. 10. An abnormal "proembryo-like" embryonic structure found in the region of fertilized archegonia. ×130.

FIG. 11. A young embryo complex with embryonic units, "proembryo-like" structures, and large, abnormal, multinucleated spherical cells. Further explanation in text. ×115.

micropyle; and at an early stage the cells of this region are dead and empty, the growth of the integument continuing only at its base (Saxton, 1909, fig. 1). After pollination, a layer of small, densely cytoplasmic cells in the inner proximal lining of the micropyle grow actively and narrow the micropylar opening at this end (Saxton, 1910a, figs. 2 and 3). The micropyle, however, is never completely closed.

The young nucellus shows a differentiation into two regions: a peripheral portion and a central portion. Saxton (1909, figs. 3 and 4) states that the central portion is composed of sixty-four slightly larger cells, the megasporocytes, containing scanty cytoplasm. Most conifers do not demonstrate such a large number of megasporocytes; therefore, it would be better to call this region, as usually termed, the spongy tissue.

The mature ovules (fig. 5) are ovoid, curved and bear two unequally developed wings. The upper portion of the ovule is elongate and narrow and the nucellus extends far up into the narrow tip. Likewise, as seen in figures 21 and 26, the megagametophyte narrows down and extends to the very tip of the narrow micropylar end of the nucellus.

The mature nucellus may be considered to have four regions. The external region is composed of a single layer of vertically elongated, rather thick-walled, darkly-staining, and probably dead cells making up the epidermis. The peripheral region within the epidermis is composed of vertically elongated to isodiametric, lightly staining, uninucleate, living cells. The innermost region is the megaspore and its contained gametophyte, and outside of this region is a layer of yellow, partially disintegrated and digested cells (figs. 21 and 22).

The ovulate cones usually produce 20 to 30 ovules, a large percentage of which are abortive. The ovules in the center of the cone—or those situated apparently on the center of each scale—mature, while those situated more laterally, tend to abort. From a mature cone containing just twenty ovules, four ovules were abortive. One scale bore six ovules, two of which were abortive, three had very young embryos, and one possessed a well developed embryo. The opposite scale bore five ovules, one of which was abortive, one had a fairly well developed embryo, and the remainder were poorly developed. The third scale bore one ovule with a well developed embryo, and four with poorly developed embryos. The fourth scale bore five poorly developed ovules, one of which was abortive. This is a typical example of the conditions found in all ovulate cones, although the percentage of abortive ovules is often greater.

In conifers, typically, all of the ovules develop at the same rate. It is possible that in *W. cupressoides*, and the Callitroideae, in general, the ovules develop at different rates from the beginning; or, it is also possible that the ovules develop at the same rate up to a certain stage, as in most conifers, and then one ovule tends to speed up its development while the others abort. Further, the embryos in the abortive ovules, instead of dis-

integrating, as in other conifers, remain in the condition at which they ceased development.

THE MICROSPORE UP TO POLLINATION AND GERMINATION

No description in the literature of the development of the microsporangium or the early microspore could be found. The author examined numerous pollen grains from mature male cones and can verify Saxton's statement (1910a) that the mature pollen grain is uninucleate at the time of shedding. No prothallial cells are formed.

Saxton's (1909) description of the germination of the pollen grain is quite complete and is here summarized. The pollen grain has a fairly thin cellulose endospore and a very thick, hard exospore. As many as three pollen grains germinate on the nucellus to form pollen tubes, but in no case has more than one pollen tube been seen to complete its development. The author, however, observed in many cases two fully developed pollen tubes which had penetrated the megagametophyte.

Continuing with Saxton's description, at germination, the exospore grows and applies itself closely to the nucellar surface. There is, however, no immediate growth of the endospore or development of a tube. Later, after the initial growth of the exospore, the endospore grows through it, forming the pollen tube which penetrates the nucellus at once. The single nucleus passes into the young tube. The next stage observed by Saxton shows the pollen tube with generative and tube nuclei within the apex of the nucellus.

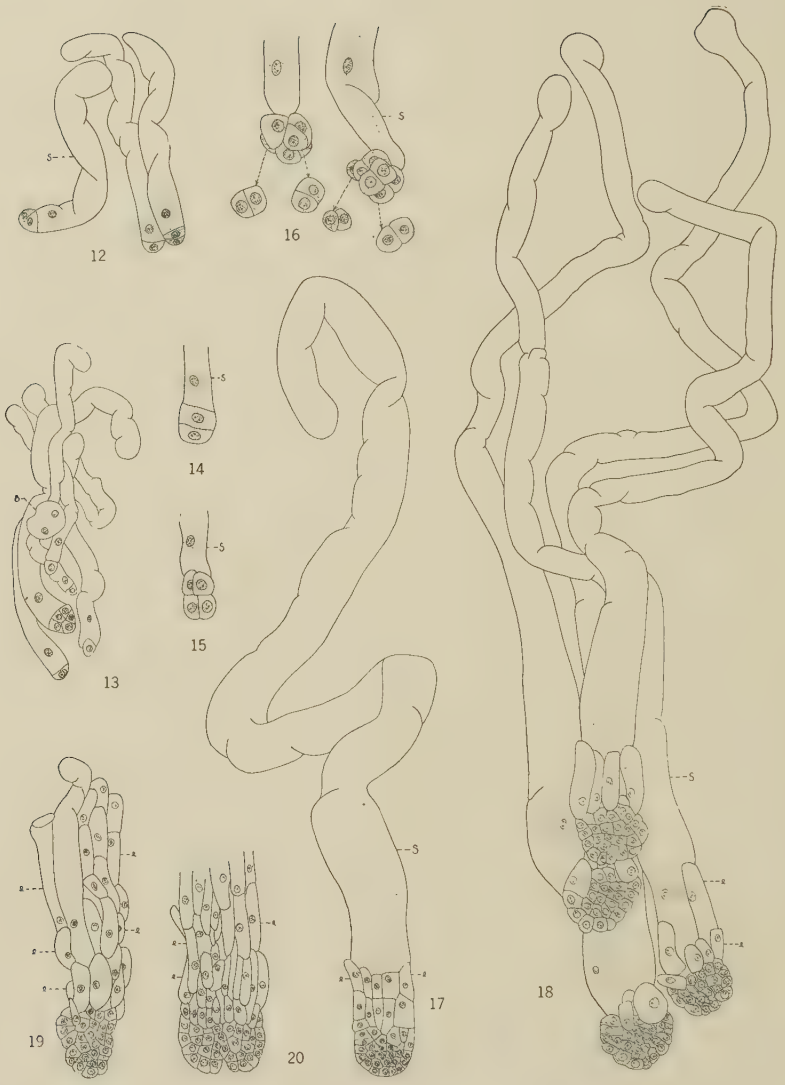
MEGASPOROGENESIS

Since the author did not observe megasporogenesis, Saxton's (1909, 1910a) account is summarized here [see especially fig. 5 (1909) and figs. 3–5 and 7–13 (1910a)]. Some time after pollination, the spongy tissue of about sixty-four cells (megasporocytes, according to Saxton, 1909) at the base of the nucellus is organized. Later, in this region, a single functional megasporocyte becomes discernible by its larger size, its slightly thicker wall, and the enlargement of its nucleus. Still later, a tapetal layer is evident.

About a week later, the functional megasporocyte may be seen in synapsis. The actual reduction division was not observed, and it is yet uncertain whether three or four megaspores are formed. It is certain, however, that only a single megaspore becomes functional; and it is probable that the megaspore which becomes functional is not the lowest megaspore of the linear tetrad or triplet. The wall of the megaspore becomes extremely thin.

THE EARLY DEVELOPMENT OF THE MEGAGAMETOPHYTE

The first division of the megaspore nucleus was seen by Saxton (1910a, fig. 15); at this stage, the nuclei demonstrate no polarity and are central



FIGS. 12 and 13. Young embryonic units composed of a primary suspensor and one-, two-, or few-celled embryos. ×125.

FIG. 14. A single two-celled embryo on the end of its primary suspensor. ×200.

FIG. 15. A single four-celled embryo on the end of its primary suspensor. ×200.

FIG. 16. Young embryos of few cells on the ends of their primary suspensors. ×810.

FIG. 17. A young multicellular embryo with the first indications of a secondary suspensor composed of embryonal "tube" cells. ×940.

FIG. 18. Young multicellular embryos at about the same stage of development as in fig. 17. ×1000.

FIG. 19. A young multicellular embryo with a multicellular secondary suspensor which is still incompletely developed. The individual cell ("embryonal tube") unit of the secondary suspensor is indicated by the letter 'e.' ×900.

FIG. 20. A young multicellular embryo similar to the one shown in fig. 19, but also showing late cleavage or budding. ×880.

and not parietal in position. After the second division, the nuclei are parietal in position, protrude inwardly from a thin layer of cytoplasm, and indicate polarity as two become situated at the lower end and two near the upper end of the prothallus (Saxton, 1910a, fig. 16).

The inner cells of the nucellus and the disintegrating spongy tissue act as a food supply for the development of the megagametophyte. Certain cells in the axis of the nucellus break down forming a path for the growing prothallus. The subsequent divisions of the prothallus have not been seen, but a 64-celled stage of free, parietal nuclei has been observed (Saxton, 1910a). The nuclear divisions are indubitably simultaneous and Saxton believes that the divisions proceed at intervals during a period of three months. The nuclei project slightly into the large central vacuole, but later the cytoplasm thickens and surrounds them. Figure 21 shows quite clearly the upper portion of a nucellus containing a peripheral layer of megagametophytic, free nuclei surrounding the central vacuole. The author has estimated this stage as being that of 256 free nuclei.

FURTHER DEVELOPMENT OF THE MICROGAMETOPHYTE AND MEGAGAMETOPHYTE

The pollen tube usually reaches the megagametophyte while the latter is still in the free-nucleated stage (fig. 21). Saxton (1910a) has also seen a pollen tube in contact with the four-nucleated megagametophyte, and he has recorded several instances where a three-nucleated pollen tube had penetrated the nucellus before megaspore germination.

Eventually, the prothallus grows upward into the nucellar apex, almost reaching the apex itself (figs. 21 and 26). Wall formation in the megagametophyte occurs as in the majority of other conifers (Saxton, 1909). The inward growth of alveoli is controlled by the nuclei which are connected by nuclear spindles. The mature, completely closed gametophytic tissue cells radiate outward from the center in a very regular arrangement (fig. 22). The original alveolar walls persist in the mature gametophyte and the mature cells arise by divisions of these original cells (Saxton, 1909). Any further description of the megagametophytic development seems unnecessary, as it is typical for conifers, a type which Sokolowa (1880) has so adequately described.

According to Saxton (1909), the pollen tube rarely penetrates the apex of the prothallus but enters a short distance below the apex before wall formation begins. It is more likely that the pollen tube does not penetrate the megaspore membrane at all until the time of fertilization. It is now believed that, as in *Callitris* (Looby and Doyle, 1940), the pollen tube originally forms a groove in the megaspore membrane, and that the groove deepens, the two edges of it coming in contact outside of the pollen tube. According to the author's observations, this interpretation is correct, as

the pollen tube contacts and grows down beside the megagametophyte while it is still in the free nuclear stage. A partial or complete encirclement of the pollen tube occurs, therefore, but the megaspore membrane is not ruptured until fertilization.

Figure 21 shows the pollen tube in contact with the young, free-nucleate megagametophyte; and, although it is difficult to distinguish the megaspore membrane, no prothallial nuclei can be seen outside of the tube at this stage of development. The author has followed the pollen tube as it appears in a series of sections. The megagametophytic nuclei nowhere completely surround the pollen tube; and, at this stage, the tube has not penetrated the megagametophyte. Numerous other cases of ovules have been seen by the author in which the pollen tube passes at least one-half of the distance down between the megagametophyte and the nucellus before it apparently enters the former. Thus, it seems more likely that the female prothallus "rolled around" the pollen tube enclosing it, as is the case in *Callitris*, instead of the pollen tube penetrating and growing into the female prothallial tissues.

By the time the pollen tube has reached one-half or one-third of the distance down the megagametophyte, the body-cell and the two sterile nuclei are present (figs. 23 and 24). The stalk nucleus is very small, with a dark nucleolus, and is imbedded in a small mass of cytoplasm (fig. 23). The tube nucleus is equally as small and only slightly in advance of the other two (fig. 24). The body cell is considerably larger than the sterile nuclei and it has a dark-staining, granular cytoplasm, and a small, lightly staining nucleus in the center (fig. 23). The membrane of the pollen tube thickens within the megagametophyte, but this increase in thickness may be partly due to the close association of the megaspore membrane with the tube wall.

At this point, a note about the megaspore membrane seems in order. As might be expected in a highly evolved conifer, the megaspore membrane is quite thin. Measurements taken on the membrane at the time of the free nuclear stage of the megagametophyte gave a thickness of 0.5 microns at a position about one-half to two-thirds the distance away from the micropyle. The thickness of the megaspore membrane around a mature female prothallus, at a position about two-thirds the distance from the micropyle, is 1.2 microns. A single ovule was examined to obtain the measurement at the free nuclear stage, but the above measurement for the mature ovule is an average taken from ten observations on as many ovules.

ARCHEGONIAL FORMATION

Soon after the cell formation of the megagametophyte is complete, the archegonial initials make their appearance. They may be easily distinguished by their considerably larger size, and their slightly larger nuclei (Saxton, 1910a, fig. 22).

The archegonia in the Callitroideae are lateral in position, and usually adjacent to the pollen tube or tubes. In regard to the lateral position of the archegonia, questions often arise. Is the lateral position of the archegonia determined by the method of growth of the pollen tube? If no pollen tube developed at all, would the archegonia arise in a terminal or lateral position? Answers to these and similar questions are given in the following quotation from Saxton's paper on *Actinostrobus* (1913a).

> The formation of archegonium initials in their normal position, laterally and deep-seated in the prothallus, is not determined by the position of the pollen tube, but this position does determine which of the very numerous archegonium initials become functional archegonia.
>
> Considerable stress has been laid on this point, since it must be emphasized that in *Actinostrobus* and *Callitris*, and doubtless also in *Widdringtonia*, although not proved in that genus, the position of the archegonium initials is a definite character of the female gametophyte, and not merely correlated with the position of the pollen tube.

In his early paper (1909), Saxton expresses considerable doubt as to the existence of archegonial neck-cells and concludes that they are not formed. In his second paper (1910a), however, he shows a drawing of the archegonial neck-cells, but he does not sufficiently describe them in the text. The author has definitely ascertained that four archegonial neck-cells are formed in a single tier (fig. 25 shows them in transverse section, and figs. 23, 24, and 26 show them in longitudinal section). After fertilization, however, no neck-cells can be found; and it is probable that the neck-cells are ephemeral and disappear shortly before or at the time of fertilization.

The number of archegonia varies considerably. According to Saxton (1910a) there may be as few as 25 to 30 and sometimes as many as 100, though they vary usually between 40 and 70. In the ovule from which the previously mentioned photomicrographs were made, there were approximately 30 to 40 archegonia in the basal, functional group (figs. 23, 24, 25) and from 50 to 70 stretched along the pollen tube at different intervals between the micropylar end and the basal group (fig. 26). For comparison, Saxton (1909) counted as many as 200 archegonia in *W. juniperoides*.

The archegonia are lateral and deep-seated in the prothallus. They extend in a row from near the tip of the prothallus to one-half or two-thirds the distance down the prothallus (fig. 26). Around the terminal, swollen vesicle of the pollen tube, a large number of archegonia, 15 to 30, or more, become grouped (figs. 23, 24, 26). Each archegonium of the group is in direct contact with its neighbor, and in no cases are individual archegonial jacket cells present. Around the whole basal group of archegonia, however, a slightly differentiated jacket may be observed (figs. 23 and 24). All of the archegonia of the basal group are well developed; but the remaining archegonia usually do not mature, and they disintegrate soon after fertilization.

Out of thousands of archegonia examined by Saxton (1909, 1910a), only one archegonium showed the presence of a structure which simulated a

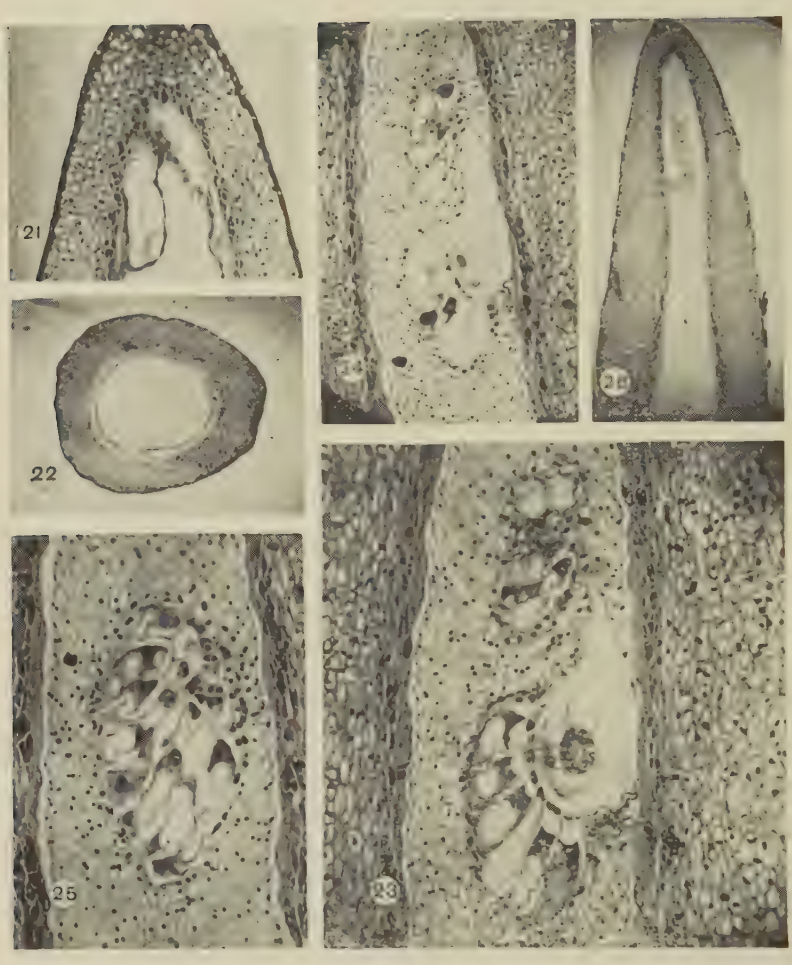


FIG. 21. The upper portion of a longitudinal section of an ovule in which the gametophyte is at about the 256-free-nucleated stage. Notice the pollen tube in contact with the free nuclei. ×90.

FIG. 22. A cross-section of a mature ovule to show the relative proportions of the gametophyte and the regions of the nucellus. Notice, also, the radial arrangement of the mature megagametophytic cells. ×25.

FIG. 23. The basal, functional group of archegonia in contact with the terminal vesicle of the pollen tube. Notice the archegonial structure, the body-cell and stalk-nucleus in the pollen tube. Longitudinal section. ×135.

FIG. 24. Similar to fig. 23, but the tube-nucleus is now visible. ×85.

FIG. 25. A longitudinal section of the megagametophyte showing the archegonial neck-cells in cross-section. Notice the four neck-cells in a single tier. ×145.

FIG. 26. A longitudinal section of an ovule (integument removed) showing the archegonia arranged along the pollen tube. Notice the basal group of functional archegonia around the terminal vesicle of the pollen tube. ×25.

ventral canal-nucleus. The author, likewise, could find no case where it could be stated that a ventral canal-nucleus was present.

The mature archegonium consists of a large, spherical, centrally situated oosphere nucleus, and rather dense cytoplasm with a large basal or partially lateral vacuole (figs. 23 and 24). The neck-cells do not persist for very long, and the archegonia of the basal group finally open into the terminal vesicle of the pollen tube.

THE MATURE MEGAGAMETOPHYTE

The cells of the mature megagametophyte vary in the number of nuclei they contain. Directly after cell-wall formation is complete, each cell is uninucleate; but, a later stage will show cells containing two, three, or more nuclei as well as a single nucleus (figs. 6 and 7). The author observed an occasional occurrence of five-nucleate cells. The binucleate or multinucleate condition arises as a result of normal mitotic divisions of the original nucleus at about the time the archegonia are matured. To some, this might indicate that all the cells of the megagametophyte are potential archegonia. The multinucleate condition persists to the maturity of the seed.

THE MALE NUCLEI AND FERTILIZATION

Saxton (1910a, figs. 36 and 37) observed only one preparation in which the two male cells were completely organized. Each male cell is approximately hemispherical and consists of a dense and homogeneous cytoplasm, a large centrally placed nucleus with no nucleoli, and a definite cell wall membrane.

The actual process of fertilization was not observed, but both male cells are functional, as two archegonia are fertilized by the contents of a single tube.

THE PROEMBRYO

Probably the only important phase of the life history of *Widdringtonia cupressoides* that is not yet fully understood is that of the proembryo. Guided by the known facts of closely related genera, however, and by what we do know about this species, we may, somewhat speculatively, fill in the gaps of our knowledge.

The early phases of the proembryo have been described by Saxton (1909, 1910a, 1934). The first stage of the proembryo observed is that of two free nuclei arranged lengthwise in the archegonium (Saxton, 1910a, fig. 38). No starch is present at this stage, although in later stages an abundance may be seen.

The critical stages of proembryonic development have not yet been observed. Although a five-nucleate proembryo and a ten-celled proembryo have been recorded by Saxton, the intervening stages are still unknown.

In the five-nucleate stage (Saxton, 1910a, fig. 39), spindle fibers have been seen between the upper four nuclei indicating that they probably had a common origin from the upper nucleus of the two-nucleate stage.

The completed proembryo is probably the ten-celled stage which completely fills the archegonium (Saxton, 1909, fig. 16). How this condition arose from the five-nucleate stage is not understood.

FURTHER DEVELOPMENT OF THE EMBRYO

The proembryonic stage is brought to a close with the elongation of the suspensors. Unfortunately, this most important stage of the embryogeny has not yet been observed, either by Saxton or by the author. Every other important stage in the embryogeny is now known.

In his earlier papers (1909, 1910a) Saxton intimated that only a single embryo was formed by each proembryo, and that the extra cells of the proembryo disintegrated. We already know (Schnarf, 1933; Strasburger, 1872, 1896; Hofmeister, 1863) that in many of the Cupressaceae, where the archegonia are grouped together in a complex, a pollen tube containing two functional sperms may fertilize two adjacent archegonia, one sperm entering each archegonium. We also know that in *Widdringtonia cupressoides* two pollen tubes may reach maturity. If one pollen tube reached maturity, and if only one embryo developed from each fertilized egg, two embryos would be formed. If two pollen tubes reached maturity, then four embryos would be developed. Four embryos would, therefore, be the highest number that could be found in a single ovule.

That such a condition is impossible has now been proved. The author counted up to sixteen embryos per ovule, with a possibility of more. In his later paper (1934) Saxton states that the proembryo cleaves into a number of units. It is believed by the author that each proembryo forms at least four embryo units as in *Actinostrobus* (Baird, 1937; Saxton, 1913a). With the presence of two pollen tubes, this would allow for the sixteen young embryos that have frequently been encountered. Eight embryos, also, are often formed, indicating that in these instances only one pollen tube developed to maturity. To substantiate such a claim, the author has counted the total number of embryos produced per ovule for a large number of ovules. Table 2 will clarify the statement that eight to sixteen embryos may be produced in one ovule.

TABLE 2

Embryos per ovule	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Ovules with above number of embryos	11	9	9	16	11	11	15	13	7	8	8	0	6	5	5	9

The first two items in this table should, perhaps, not have been included, as they represent the counts of nearly mature embryos where the smaller embryos would already have been destroyed. In the ovules containing 3

to 8 embryos, we may assume that a single pollen tube reached maturity, thus fertilizing two archegonia which would give rise to two embryo systems. Similarly, in ovules containing 9 to 16 embryos, probably two pollen tubes reached maturity, supplying a total of four sperms. Four archegonia might therefore be fertilized which, if four embryos developed from each fertilized egg, would give rise to a total of sixteen embryos.

Each embryonic unit of the early embryo consists of a single, long, coiled and undivided primary suspensor cell and a terminal one-celled embryo (figs. 11, 12, and 13). It is safe to assume that these two cells arose from a single proembryonic cell (or embryo initial), and that a prosuspensor (equivalent to a complete embryo initial) is missing.

Because of crowding, possibly, not all of the embryo units develop. When a normal elongation of the primary suspensor fails to occur, and the embryo unit instead divides abnormally, chains of cells are frequently produced in the region of the functional archegonia (fig. 8). Normal embryos are usually produced from the same region of functional archegonia. Occasionally, an embryo unit will elongate abnormally, and the nucleus will divide several times; but no cell walls will be formed (fig. 9).

Other structures that look like proembryos (figs. 10, A and 11, A) may be seen at the level of the functional archegonia, one or two of which have produced additional normal embryos. Saxton (1910a) also records similar structures, but offers no plausible explanation. These structures apparently do not produce normal embryos, but become septated into several cells each containing one or two nuclei. They are about the size of an archegonium, and they may be archegonia that have developed abnormally, possibly parthenogenetically, in some unexplained manner.

Large, abnormal spherical cells containing several free nuclei, often observed in the region of the basal group of archegonia, are thought to be whole embryo units or embryo initials, that, instead of dividing to form an embryo cell and a primary suspensor cell, enlarged greatly to form an abnormally swollen, multinucleate cell. A few of these structures are indicated by the letter B in figures 8, 11, and 13.

It is possible, therefore, that more than four embryos are produced from each ten-nucleate proembryo. At least it may be supposed that some of the stunted and abnormal embryonic structures arose from some of the upper proembryonic cells, which may be considered as comparable to rosette cells and rosette embryos respectively. We may conclude, then, that cleavage polyembryony is the rule. Whether the type is determinate or indeterminate cannot be stated with certainty, since this depends on a precise knowledge of the proembryo and the earliest stages of suspensor elongation.

As observed by the author in all cases, but contrary to Saxton (1934), the first division of the one-celled embryo, after suspensor elongation has

begun, is transverse to the long axis of the suspensor. The upper of these two cells cannot be considered the first embryonal cell of the secondary suspensor, as the second division is longitudinal—at right angles to the first division—and cuts the first two cells into two cells each. The two-celled embryo may be seen in figures 12 and 14. Figure 15 shows the four-celled embryo at the end of its primary suspensor. In the author's opinion, apical cell growth may be said to exist only through the two-celled stage, as further divisions are evidently stimultaneous for a time in all of the cells. The cells produced by the third and fourth divisions are loosely arranged, and it seems that the individual cells may move about on each other to some extent.

Figure 16 represents two young, few-celled embryos showing, in particular, the irregular arrangement of the cells. As it is difficult to show all the cells of an embryo mass in a single drawing, the cells at a lower plane of focus than that of the principal drawing are drawn to one side.

Eventually, a massive secondary suspensor, consisting of hundreds of small, rectangular, box-like embryonal "tubes" is formed. These cells are formed by the growing region of the embryo; but, instead of becoming a part of the embryo proper, they elongate and become the cells of the secondary suspensor. Figure 17 is a drawing of a single embryo unit with a young multicellular embryo, its primary suspensor (S), and the beginnings of a secondary suspensor composed of a few embryonal "tubes" (e). Figure 19 shows four embryos of an embryo complex at a slightly later stage of development.

The cells of the secondary suspensor project back over, and surround the end of, the primary suspensor (fig. 18). Figures 19 and 20 depict two more highly developed embryos in which the secondary suspensors are composed of numerous, small, elongated cells projecting back over the primary suspensor. The secondary suspensor of a mature embryo consists of thousands of such cells. The relative length of the secondary suspensor varies; in two embryos, whose embryos proper are at about the same stage of development, the secondary suspensor of one may be twice as long as that of the other.

The embryo proper (that portion of the embryonic unit that will form the mature embryo, exclusive of the suspensor system) is at first pointed or rounded and narrower than that of the secondary suspensor which bears it. Later the embryo broadens and its tip becomes more rounded. Eventually, two cotyledons and a plumule tip are differentiated, the cotyledons as two lateral bulges at the apex with the stem tip or plumule between the two. It is not definitely known whether the cotyledons or the plumule are differentiated first. The embryo proper, until late in development, is of about one-eighth to one-quarter the volume of the secondary suspensor.

If a longitudinal section is made of a fairly mature embryo proper, a

central cell or "key-cell," from which the other cells radiate may be demonstrated.

Frequently budding, or late cleavage, occurs in the multicellular embryo. Two embryos are formed from a single one by the divergence of two main regions of growth. Such a condition may be seen in figure 20.

Occasionally three, instead of two, cotyledons may be formed. This phenomenon will be mentioned again in connection with germination.

THE GERMINATION OF THE SEED

At germination, according to Saxton (1910a), the testa is often carried up on one of the cotyledons. The plumule first develops a pair of opposite leaves at right angles to the cotyledons. These are followed by three to ten alternating whorls of leaves, each whorl with four linear, elongated, flattened juvenile leaves. Later, on the juvenile shoots, the leaves become spirally arranged (Florin, 1930). In the tricotyledonous seedlings, the three equally developed cotyledons are succeeded by alternating whorls of three leaves each.

Hill and de Fraine (1908) report further details on the seedling. The normal root has a diarch, exarch protostele, and the transition from stem to root follows Van Tieghem's Type 3. The single vascular bundle of each cotyledon undergoes a bifurcation accompanied by a rotation of the xylem so that the protoxylem becomes exarch. The opposing phloem masses fuse in pairs. In the tricotyledonous seedlings, the diarch root is also present, as the xylem strands of two of the cotyledons fuse to form a common mass. Morris (1909–1910) has described the occurrence of an abnormal twin seedling.

TIME OF DEVELOPMENT

A long period of fourteen to fifteen months intervenes between pollination and fertilization. There is no break, however, in the continuity of development as in most conifers of temperate regions that are pollinated in one season and fertilized in the next; therefore there are no fixed periods when definite stages may be obtained.

CHROMOSOMES

Saxton (1909) states that the diploid chromosome number is 12 or 14 and that the haploid number is 6 or 7. Sax and Sax (1933), however, report that the basic chromosome number (haploid) of the Cupressaceae, as represented by *Chamaecyparis*, *Thuja* and *Juniperus*, is 11. It seems likely that Saxton was inaccurate, and that the haploid number is probably 11 or 12.

THE PHYLOGENY OF THE CUPRESSACEAE

The author has compiled in chart form considerable data on the reproductive morphology and embryogeny of the twelve important and better

known genera of the Cupressaceae. All the characteristics used in the chart are of phylogenetic importance; thus, by careful consideration, it is possible to draw from the chart several important phylogenetic conclusions.

In most cases the characteristics are presented in pairs, the first of each pair being the primitive, and the second the advanced characteristic. In a few cases, where three items are entered, the second one is an intermediate characteistic which manifests itself as transitional between the primitive and the advanced phase. From the chart, Table 3, the genera, and also the sub-families as entities, may be compared.

In deciding which of the characteristics are primitive and which are advanced, the author has referred to a number of articles. In the second vertical column following each pair of characteristics, the articles discussing the respective characteristics are indicated by number. In the last horizontal column, each group of numbers indicate the sources of information referred to the genus listed directly above at the top of the table. The numbers refer to the respective authors' names listed in the footnote.

Only three symbols have been adopted to fill out the table. A plus sign (+) indicates that the characteristic horizontally opposite is present in the genus or sub-family listed vertically above. The letter 'M' indicates that the majority of the species of the respective genus (or of the genera of the respective sub-family) possess the characteristic horizontally opposite. In the Thujoideae, *Tetraclinis* and *Fitzroya* present many transitional characteristics between the Thujoideae and the Callitroideae. To emphasize this, a third symbol, the letter 'T' has been used.

The first topic to be discussed is one of taxonomic significance. On the basis of the data presented in Table 3 and on two items mentioned by Saxton, the author supports Saxton's (1910b) opinion that *Callitris*, *Actinostrobus* and *Widdringtonia* be established as a distinct sub-family, the Callitroideae, within the family Cupressaceae. By referring to Table 3 and to Saxton (1910b), it will be noticed that the genera composing the proposed Callitroideae differ from all other genera of the Cupressaceae in the following morphologically diagnostic characteristics: archegonia lateral in position (item II), the absence of a prosuspensor in the embryo (item IV), a proembryo that completely fills the archegonium (item V), the absence or obscurity of an archegonial jacket (item VIII), a proembryo which is not in definite tiers (item IX), ovulate cone scales all fertile instead of some sterile as in other members of the Cupressaceae (Saxton, 1910b) and male nuclei equal in size to the female nulcei instead of smaller as in other genera of the Cupressaceae (Saxton, 1910b).

Pilger (1926) divides the Cupressaceae into three sub-families: the Thujoideae (including members of the proposed Callitroideae), the Juniperoideae and the Cupressoideae. In view of a definite segregation of the Callitroideae from the Thujoideae of Pilger's classification, the author suggests the revision below.

TABLE 3

Characteristics	Citations on phylogenetic status of the characteristics			Cupressus	Chamaecyparis	Juniperus	Biota	Libocedrus	Tetraclinis	Fitzroya	Thujopsis	Thuja	Actinostrobus	Callitris	Widdringtonia	Cupressoideae	Juniperoideae	Thujoideae	Callitroideae
I. Only ventral canal-nucleus formed	8	16	—			+	+	+	+	+			+	+			+	M	M
Neither ventral canal-nucleus or -cell formed			—									+			+				
II. Archegonial complex usually in terminal position	10	21	—	+	+	+	+	+			+	+				+	+	M	
Archegonial complex usually terminal, rarely lateral	32	33	—						+	+								T	
Archegonial complex usually lateral in position			—										+	+	+				+
III. Embryogeny demonstrates cleavage polyembryony	3	4	—	+	+	+	+	+	+	+	+		+	+	+	+	+	M	+
Embryogeny demonstrates simple polyembryony	5	7	—								+	+							
IV. Primary suspensor and prosuspensor present			—	+	+		+	+								+		+	
Prosuspensor present, primary suspensor absent or obscure	5	38	—			+			+?		+	+					+	+	
Prosuspensor absent, primary suspensor present			—										+	+	+				
V. Mature embryo with polycotyledony	2	9	—	M					+							+			+
Mature embryo with dicotyledony, usually	17		—		+	M	M	+		+	+	+	+	+	+	+	M	M	+
VI. Proembryo does not fill the archegonium	5	38	—	+		+	+	+	+		+	+				+	+	M	
Proembryo completely fills the archegonium			—							+			+	+	+			T	+
VII. More than four neck-cells in the archegonium	10	16	—	+	+			+	+		+	+				+		+	
Usually four (or fewer) neck-cells in the archegonium			—			+	+			+			+	+	+		+	+	+
VIII. Archegonial complex with a common jacket	10	32	—		+	+	+	+	+	+	+	+				+	+	+	
Common jacket absent or obscured	33		—										+	+	+				+
IX. Proembryo in tiers	10	38	—	+	+	+	+	+	+	+	+	+				+	+	+	
Proembryo not in tiers			—										+	+	+				+
X. Pollen grain 2-nucleate at the time of pollination	3	10	—	+	+		+	+			+	+				+		M	
Pollen grain 1-nucleate at the time of pollination	38		—			+			+	+			+	+	+	+	+	T	+
Literature sources for information obtained on the respective genera listed above. See footnote.				9	6	9	9	9	9	9	31	3	1	9	9				
				13	20	12	11	22	36	15	38	4	9	21	17				
				14	39	24	38	24	38	24	40	5	24	23	24				
				18		26		38		38		9	35	24	25				
				19		27						11	38	34	32				
				22		28						24			33				
				24		29						38			34				
				31		30									37				

1, Baird (1937). 2, Buchholz (1919); 3, (1920); 4, (1926); 5, (1929); 6, (1932); 7, (1933); 8, (1940). 9, Butts and Buchholz (1940). 10, Chamberlain (1935). 11, Cook (1939a); 12, (1939b). 13, Doak (1932); 14, (1937). 15, Doyle and Saxton (1933). 16, Eames (1936). 17, Hill and de Fraine (1908). 18, Hofmeister (1863). 19, Juel (1904). 20, Land (1902). 21, Lawson (1904); 22, (1907). 23, Looby and Doyle (1940). 24, Masters (1895); 25, (1905). 26, Mathews (1939). 27, Nichols (1910). 28, Noren (1904); 29, (1907). 30, Ottley (1909). 31, Pilger (1926). 32, Saxton (1909); 33, (1910a); 34, (1910b); 35, (1913a); 36, (1913b); 37, (1934). 38, Schnarf (1933). 39, Sugihara (1938); 40, (1939).

Family Cupressaceae
Sub-family Cupressoideae
Genera: *Cupressus, Chamaecyparis*
Sub-family Juniperoideae
Genera: *Juniperus, Arceuthos,* Microbiota**
Sub-family Thujoideae
Genera: *Libocedrus, Biota, Tetraclinis, Fitzroya, Thujopsis, Thuja, Diselma,* Fokienia**
Sub-family Callitroideae
Genera: *Actinostrobus, Callitris, Widdringtonia, Callitropsis**

The position of the Cupressoideae as lowest in the family seems justified in view of the fact that this sub-family possesses the greatest number of primitive characteristics—at least nine of the ten items are primitive (items II, III, IV, V, VI, VII, VIII, IX, and X).

The Juniperoideae, likewise, are low in phylogenetic position, since at least six of the ten items are primitive (items I, II, III, VI, VII, and VIII). The Juniperoideae occupy a slightly higher position because the primary suspensors of the embryos are obscure or absent (item IV) and dicotyledony has been attained in the majority of the species (item V). The Juniperoideae also have archegonia with a reduced number of neck-cells, a character which is definitely an advanced one (item VII).

The Callitroideae possess the greatest number of highly evolved characters (items II, IV, V, VI, VII, VIII, IX, and X). Six of these characteristics are definitely advanced as opposed to only four advanced in the Thujoideae (items V, VI, VII, and X). Some of the advanced characteristics seen in the Thujoideae are possessed by only two genera, notably *Tetraclinis* and *Fitzroya*. As a whole, then, the Callitroideae are far more advanced than the Thujoideae.

The author is of the opinion, however, that the genus *Thuja*, on the basis of all its characteristics, occupies a phylogenetic position equal to that of the sub-family Callitroideae. This position is based on a consideration of items I, III, and V. The fact that no ventral canal-nucleus is formed in *Thuja*, and the fact that it has reached simple polyembryony and dicotyledony in evolution places it as the highest evolved member of the Thujoideae. Such a conclusion is based, of course, upon the assumption that simple polyembryony, dicotyledony, and the lack of a ventral canal-cell or ventral canal-nucleus are characteristics of greater phylogenetic value than the other items listed in the chart.

In the Thujoideae *Libocedrus* and *Biota* possess the greatest number of primitive characteristics: eight of ten items are primitive (items I, II, III, IV, VI, VII, VIII, IX and X).

* Genera incompletely known, or of doubtful status.

Next to *Thuja*, *Fitzroya* possesses the greatest number of advanced characteristics (items II, V, VI, VII and X). *Thujopsis*, as a genus, however, has reached simple polyembryony and dicotyledony; and, although it has a total of only three advanced characteristics (items III, IV, and V), the author believes that it should stand next to *Thuja* in phylogenetic position. *Tetraclinis*, with its total of seven primitive characteristics, should stand low in the phylogenetic scale (items I, III, V, VI, VII, VIII, and IX).

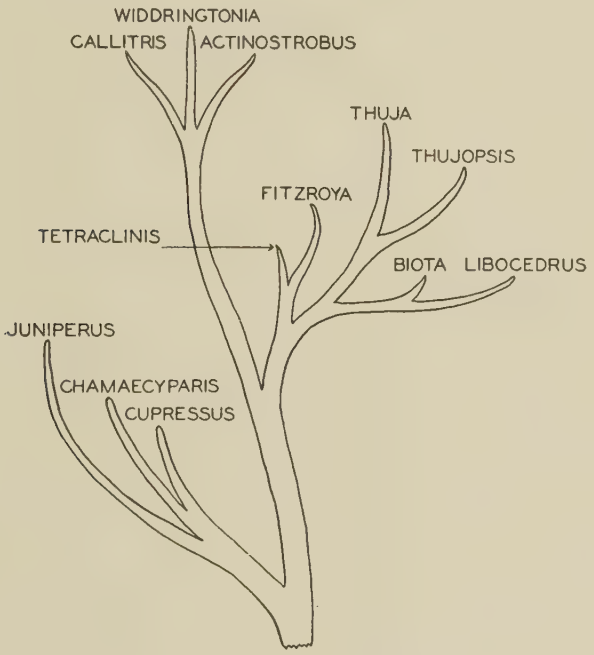


FIG. 27. A phylogenetic diagram of the Cupressaceae.

Nearly all the genera of the Callitroideae have advanced characteristics, although the group still retains cleavage polyembryony as an outstanding primitive characteristic (item III). *Widdringtonia* is slightly more advanced than the other two genera in that it has lost the tendency to form a ventral canal-nucleus.

It is of importance to note that the Callitroideae possess outstanding characteristics that distinguish them from the other groups of the Cupressaceae. These characteristics have already been mentioned. It is of interest, however, to compare the Callitroideae with *Fitzroya* and *Tetraclinis*. *Fitzroya* possesses a proembryo that completely fills the archegonium, a one-nucleate mature pollen grain, occasional lateral archegonia, and a small number of archegonial neck-cells. *Tetraclinis* possesses one-nucleate

mature pollen grains, a tendency to form lateral archegonia, and four archegonial neck-cells. These characteristics, of the two genera, respectively, are found in common with the Callitroideae. From these similarities, then, we may conclude that *Tetraclinis* and *Fitzroya* are living representatives of comparable genera of past eras which gave rise to the Callitroideae.

There is no need to consider further the phylogeny of the Juniperoideae as it contains only one well known genus which we have already discussed. In the Cupressoideae, however, we may conclude from a study of the chart that *Chamaecyparis* with dicotyledony stands slightly higher that *Cupressus* with polycotyledony in several of its species.

The phylogenetic diagram (fig. 27) summarizes this discussion of the Cupressaceae. It is based on the evaluation of the generic characteristics presented.

SUMMARY

The morphology, life history and phylogeny of *Widdringtonia cupressoides* are described.

The salient features of the life history may be mentioned briefly. The cones are unisexual and the species in monoecious. The mature microspore at pollination is uninucleate; in one ovule, two pollen tubes producing two sperms each may reach maturity. One megasporocyte develops fully, and it forms three or four megaspores. The megagametophyte is formed first by free nuclear divisions and later by alveolar growth. The archegonia are numerous, deep-seated and lateral in position; each archegonium forms a single tier of four neck-cells, but forms no ventral canal nucleus.

Cleavage polyembryony is the rule. It is thought that each fertilized egg produces four embryonic units. Each unit consists of a primary suspensor and a one-celled embryo. No prosuspensor is formed. The multicellular embryo is formed by irregular divisions of a growing region. A massive secondary suspensor is formed. The mature embryo is dicotyledonous, rarely tricotyledonous.

The Callitroideae, containing the genera *Actinostrobus*, *Callitris* and *Widdringtonia*, are regarded as a natural group which should be established as a distinct sub-family of the Cupressaceae on the basis of the following distinguishing characters: archegonial complex lateral in position, absence of a prosuspensor in embryogeny, a non-tiered proembryo that fills the archegonium, lack of a definite archegonial jacket, ovulate cone scales all fertile, and male nuclei equal in size to the female nuclei.

The Callitroideae are thought to be the highest evolved sub-family of the Cupressaceae because of the following advanced characters: archegonia lateral in position, lack of a prosuspensor in embryogeny, dicotyledony, only four archegonial neck-cells, a one-nucleate pollen grain and the

absence of a ventral canal-nucleus in *Widdringtonia*. The Cupressoideae and the Juniperoideae are considered the least evolved sub-families of the Cupressaceae. The Thujoideae stand between these groups, and *Thuja* is the highest evolved member of this sub-family. The Callitroideae were probably derived from an ancestral "*Fitzroya-Tegraclinis* complex" as these latter genera manifest many transitional characteristics between the Thujoideae and the Callitroideae, such as: one-nucleate pollen grains, archegonia occasionally lateral in position, a proembryo that fills the archegonium, and the presence of four archegonial neck-cells.

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Studies of the Icacinaceae. VII. A Revision of the Genus Medusanthera Seeman

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Seeman described *Medusanthera* in 1864 but later reduced it to synonymy with *Stemonurus*. It is distinct from *Stemonurus* but is identical with *Tylecarpus* of Engler, and, being older, must replace Engler's name. I transferred six species to *Medusanthera* in 1940. Two new combinations and one new species are added here. In addition, *Medusanthera australis* and *Stemonurus* (*Tylecarpus*) *Merrittii* have been segregated as the type species of two new genera. Thus ten species are now recognized in this genus.

The diagnostic characters of *Medusanthera* and its related genera are principally in the fruits. *Medusanthera* has a flattened drupe with a fleshy pulvinus or appendage borne on the concave surface. The putamen is broadly and deeply grooved on the concave surface. In addition the unisexual flowers, the pubescent filaments of the stamens, the pedunculate 2-3-chotomized inflorescences with cymose branches, the pistil with a basal gibbosity, the filaments with hairs principally on the ventral (inside) surface only, and the distinctive venation of the leaves help distinguish this genus.

Medusanthera Seeman, Journ. Bot. **2**: 74. 1864; Howard, Journ. Arnold Arb. **21**: 469. 1940.

Tylecarpus Engler, Nat. Pflanzenfam. **3**(5): 247. 1893; Sleumer, Notizbl. **15**: 246. 1940.
Lasianthera Becc. Mal. **1**: 108. 1877 in part.

Trees; leaves alternate, petiolate, exstipulate, entire, the veins pinnate, oblique to arcuate, anastomosing or rarely free; inflorescences axillary, 1–2 per node, 2-3-chotomized, the branches cymose, pedunculate, the pedicels short, bracteate, the flowers unisexual, articulated below the calyx, 5 parted; calyx cupular, obscurely 5-toothed, pubescent or glabrous, the teeth commonly ciliate; petals valvate, lanceolate-oblong, lightly pubescent or glabrous outside, glabrous inside, the apex inflexed; stamens in male flowers with subulate fleshy filaments, the filaments of functional stamens bearing long lanceolate or clavate hairs immediately below the anther when young but scattered on the upper quarter of the filament after anthesis, filaments pubescent or frequently glabrous in the female flowers, shorter than the pistil, the anthers elliptic-oblong, longitudinally introrsely dehiscent, the pistillate rudiment ovate or conical, commonly slightly compressed, undifferentiated or rarely 1-loculed, the functional pistil cylindrical, glabrous, bearing a fleshy pulviniform swelling laterally near the base, the ovary 1-celled with 2 anatropous ovules pendent from near the apex, the style short or inconspicuous, the stigma capitate, ru-

gose; drupe elliptic or oblong, the apex and base rounded or truncate, laterally compressed bearing a large fleshy pulviniform appendage on the concave surface, the convex surface 1-3-ridged, the concave surface of the putamen broadly and deeply grooved, the sarcocarp thin fleshy, not pigmented, the seed one, anatropous, pendent, the embryo minute, the cotyledons ovate or triangular, the radicle cylindrical, the endosperm copious.

Type species: *Medusanthera vitiensis* Seeman.

Distribution: Philippines, East Indies, Oceania.

The flowers of *Medusanthera* are always unisexual, not perfect and probably not polygamous as was formerly believed. The pistil is rudimentary in the staminate flowers and the anthers are sterile in the pistillate flowers. From the shape of the bud it is possible to recognize the sex of the flower. The clavate buds are usually staminate and the cucullate buds are usually pistillate. The flowers are articulated immediately below the calyx. The calyx is cupular and has indistinct teeth developed. It is rarely pubescent, more commonly ciliate on the teeth or completely glabrous. The petals are free, not fused as in *Stemonurus,* and have a typical valvate aestivation with inflexed apices. In all of the material I have examined the corolla is glabrous; however, Reinecke describes a lanate pubescence to the outer surface of the petals of *M. samoensis,* and Sleumer mentioned a pubescence on the outside surface of the petals of *M. coriifolia.* In most species of the genus there is only a slight difference in the size of the stamens in the functional female and functional male flowers. The anthers of the former are completely sterile, those of the latter are packed with pollen grains. The filaments in both are fleshy and flattened. On the filaments of the functional stamens there is a long, clavate, thin-walled pubescence. The hairs are located immediately below the anthers when the stamens are young, but after anthesis of the flower the filament elongates, and upon maturity the pubescence is scattered on the upper quarter of the filament. Reinecke believed the hairs occurred only on the lateral edges and the inner (ventral) surface of the filament, and he regarded this as a diagnostic generic character. In several of the species, however, a cluster of hairs may be found on the dorsal surface of the filament, and in some cases hairs were lacking on the ventral surface. Seeman considered eight hairs to be typical of *M. vitiensis,* but this number is not constant and usually more are found. The filaments of the sterile stamens usually have fewer hairs than those of the functional stamens. In several species, *M. glabra* in particular, no hairs are developed on the sterile stamens. The hairs are slow in developing in all species, and the younger buds may have completely glabrous stamens while the more mature stamens have a normal pubescence. The sterile stamens fall with the corolla at anthesis and therefore are not present in most specimens. In the staminate flowers the pistil is rudimentary. This rudiment is usually ovate or conical, commonly compressed, always gla-

brous, and may be undifferentiated or may contain a single sterile locule. It frequently shows evidence of a fleshy basal gibbosity on the concave side. The functional pistil is cylindric without an evident style and with a large capitate verrucose or rugose stigma. Laterally, at the base, is a fleshy gibbosity which develops into the pulviniform appendage of the mature drupe. The ovary has a single locule which is eccentrically placed, as the ovarian wall is thicker on the side bearing the gibbosity. There is no evidence of an extra locule, in the pistil, to account for the eccentric arrangement.

The fruit of *Medusanthera* is easily distinguished from that of *Stemonurus*. *Stemonurus* has an ovoid cylindrical fruit which may have a prominent groove on one side but which is not flattened. *Medusanthera* has a strongly flattened drupe which bears a large fleshy pulviniform appendage superficial to the sarcocarp. The drupe is usually oblong or ellipsoid, rounded or truncate at both ends, strongly flattened or curved, being concave on one side and convex on the other. The putamen is tenuous or woody and is strongly ridged on the convex surface. There is but one ridge on the convex surface of *M. samoensis*, but the other species have 3–5 ridges developed. On the concave surface of the putamen there is developed a large longitudinal groove. The lateral edges of the putamen extend over this groove, forming a partial cavity or locule. In the fruiting condition this cavity is filled with sarcocarp tissue. It is this cavity which has been called a second and sterile locule by many earlier authors. There is no indication of this cavity in the pistil, and it seems to be developed as the fruit matures. In the middle of this cavity extending the length of the seed is the funicle. The sarcocarp is of uniform thickness around the putamen except where it fills the cavity formed on the concave side of the fruit. Surmounting the sarcocarp is an appendage of pulvinus. This is described as whitish or porcelain in color in fresh condition. It usually equals the fruit in size and often is wider than the drupe. When dry the pulvinus shrinks and may be inconspicuous. Only one of the two ovules develops, and the seed is conformant with the shape of the locule. The raphe descends the narrow edge of the seed, 90 degrees from its course in the sarcocarp. The embryo is apical in the abundant endosperm and is extremely minute, with ovate or triangular cotyledons and a short cylindrical radicle.

The general aspect of the plant is characteristic. The leaves are generally subcoriaceous and glabrous with a characteristic pattern of venation. The inflorescence is axillary with 1–3 pedunculate 3–4-chotomized cymose inflorescences at a node.

The relationship of this genus is with *Lasianthera*, *Gastrolepis*, *Irvingbaileya*, and *Discophora* on the form of the fruit. It also has a relationship with *Stemonurus* in the wood structure and type of stamen. The similari-

PLATE I (*See opposite page for explanation.*)

ties of wood structure in these genera has been pointed out by Bailey and Howard (*Journ. Arnold Arb.* **22**: 172 ff. 1941).

Specimens cited in this study are from the following herbaria: Arnold Arboretum (A), Univ. of California (C), Gray Herbarium (G), New York Botanical Garden (NY), Singapore Botanical Gardens (S), United States National Herbarium (US). I am grateful to the directors and curators of these herbaria for the use of these materials.

KEY TO THE SPECIES

Leaves cuneate at the base.
  Corolla glabrous.
    Veins 6–9 pairs, peduncle of inflorescence 1.5–2 cm. long ..... *M. papuana*
    Veins 10 paired, peduncle of inflorescence 0.5 cm. long ..... *M. Peekelii*
  Corolla puberulous outside, veins 6–7 pairs, peduncle of inflorescence 1 cm. long .. *M. coriifolia*
Leaves rounded or acute at the base.
  Leaves 5–9 cm. long.
    Leaves ovate, the apex attenuate ..... *M. vitiensis*
    Leaves elliptic to oval, apex acute or rounded ..... *M. ovata*
  Leaves over 10 cm. long.
    Fruit 5–7 mm. long ..... *M. glabra*
    Fruit 1.3–3 cm. long.
      Fruit prominently 1-ridged ..... *M. samoensis*
      Fruit prominently 3–5 ridged.
        Leaves lance-oblong, the apex long acuminate, the veins numerous ..... *M. laxiflora*
        Leaves broadly elliptic or oblong-ovate, the apex rounded or abruptly short mucronate.
          Leaves broadly elliptic, the veins arcuate, not noticeably anastomosing . *M. carolinensis*
          Leaves broadly oblong-ovate, the oblique veins prominently anastomosing . *M. vitiensis*

MEDUSANTHERA PAPUANA (Becc.) Howard, Journ. Arnold Arb. **21**: 469. 1940.

Lasianthera papuana Becc., Mal. **1**: 108. 1877.
Tylecarpus papuana Engl., Nat. Pflanzenfam. **3**(5): 247. 1893; Schellenb., Engler Bot. Jahrb. **58**: 159. 1923; Schum. & Lauterb., Fl. Deut. Sch. Südsee 413. 1901; Pulle, Nov. Guin. Bot. **14**: 275. 1927.

Tree, 8–15 m. tall, the branches terete, short strigose to glabrate; petioles 1 cm. long, canaliculate above, short hirsute; lamina elliptic to obovate-elliptic, 14–20 cm. long, 4.5–6 cm. broad, thinly coriaceous, glabrate, the apex abruptly acuminate or obtuse, the base cuneate, the midrib sulcate above, prominent below, sparsely hirsute, the lateral veins 8–9 pairs, oblique at angle of 45 degrees; inflorescence with peduncle 2 cm. long, the cymes thin, the rhachi densely hirsute; calyx glabrous, indis-

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FIGS. 1–3, *Medusanthera glabra* (Merrill) Howard (Ramos 1628). Fig. 1, habit ×½; fig. 2, diagrammatic cross-section of the fruit; figs. 3–4, side and face view of the drupe ×1.7. Figs. 5–7, *Medusanthera samoensis* (Reinecke) Howard (Christophersen 386). Fig. 5, diagrammatic cross-section of the fruit. Notice the funicular cavity and the single ridge of the putamen; figs. 6–7, two views of the drupe showing the fleshy appendage and the single ridge of the putamen ×10. Figs. 8–13, *Medusanthera ovata* Howard (Christophersen 2166). Fig. 8, habit ×½; figs. 9–10, two views of the pistillate rudiment ×8; fig. 11, bud showing the glabrous calyx and corolla and the floral articulation; figs. 12–13, adaxial and lateral views of the fertile stamens ×8.

tinctly toothed; petals lance-oblong, 3.5–8 mm. long, 0.8–1.1 mm. wide; sterile stamens frequently glabrate, the filaments 2.6 mm. long, the anther 0.6 mm. long, the fertile stamens persistently pubescent, shorter; fertile pistil 3.6 mm. long, the pistillate rudiment conical, to 1.4 mm. long; drupe 1.1–1.3 cm. long, 0.7–.8 cm. wide, the putamen strongly 3-ridged on the convex surface.

Type collection: *Beccari* 532 from near Andai, New Guinea (not seen).

Illustrations: Beccari, Mal. **1**: tab. 3, 1877 (as *Lasianthera papuana*); Engler, Nat. Pflanzenfam. **3** (5): fig. 138. A–B 1893 (as *Tylecarpus papuanus*).

Specimens seen: New Guinea. Kaiser Wilhelmsland. *Schlechter* 16366 (C), 16432 (C), 17908 (C), 17913 (C). Nabire, Bivak, *Kanehira & Hatusima* 12863 (A), Nabire, Geelvink Bay, *Kanehira & Hatusima* 11530 (A). Celebes. *Neth. For. Service*, V-180. (A, S.)

Medusanthera Peekelii (Sleumer) comb. nov.

Tylecarpus Peekelii Sleumer, Notizbl. **15**: 237. 1940.

Tree, 7 m. tall, the branches longitudinally striate, puberulent; petioles 1.5 cm. long, puberulent; lamina oblong, 15–20 cm. long, 6–8 cm. broad, chartaceous to membranaceous, glabrous, the apex short acuminate, the ultimate apex subobtuse, the base cuneate, the midrib impressed above, prominent below, the veins 10 pairs, obscure above, slightly prominent below, ascending; cymes on peduncles 0.5 cm. long, rhachi densely hirsute; calyx cupular, 2 mm. high, indistinctly 5-toothed, glabrous; petals 2 mm. long, fleshy; fertile stamens with subulate filaments 1 mm. long, densely barbate below the anthers, anthers ovate-oblong, 0.8 mm. long; pistillate rudiment conical, to 1 mm. high; female flowers not seen; drupe oblong, 1.3 cm. long, the putamen 3-ridged on the convex surface.

Type specimen: *Peekel* 1056 (Herb. Berlin, not seen) collected near Lamekot, Lamangan, New Mecklenburg. Known only from the type.

Sleumer suggests this species differs from *M. papuana* through the more numerous lateral veins of the leaf, the smaller flowers, and the shorter and thicker male inflorescences. These differences do not seem significant, and it may be necessary, after examination of the type materials, to refer this species to synonymy with *M. papuana*.

Medusanthera coriifolia (Sleumer) comb. nov.

Tylecarpus coriifolius Sleumer, Notizbl. **15**: 236. 1940.

Tree, 5 m. tall, the branches terete, short pubescent; petioles 1.2–1.7 cm. long, distinctly canaliculate; lamina lance-oblong, 11–17 cm. long, 3–3.5 cm. broad, coriaceous, the apex acuminate, the base cuneate, the midrib immersed above, prominent below, the veins 6–7 pairs, arcuate-ascending;

peduncles of the inflorescence 1 cm. long, the pedicels of the cymose branches 1.5 mm. long, the rhachi densely appressed yellow silky tomentose; calyx cupular, 1.2 mm. high, 5-toothed; petals lance-oblong, 3.5 mm. long, subacuminate at the base, sparse yellow-pilose outside; fertile stamens with subulate filaments 3 mm. long, dilated above, bearing clavate pubescence below the anthers, the anthers elliptic 1 mm. long, the pistillate rudiment ovoid-conical; female flowers and fruits unknown.

Type specimen: *Peekel* 1604 (Herb. Berlin, not seen) collected near Lamekot, Pabaket, New Mecklenburg.

This is considered a species of uncertain position. Sleumer compared it with *S. Merittii*, which I have segregated as a distinct genus. It differs from *S. Merittii*, however, in having pubescent filaments. *S. coriifolia* is distinct in the present genus only on the "puberulous" corolla mentioned by Sleumer. In all other respects it seems identical with *M. papuana*. I have not seen material of it, but its correct position may be determined by an examination of the stem structure or the fruit when the latter is found.

MEDUSANTHERA VITIENSIS Seeman, Journ. Bot. **2**: 74. 1864.

Stemonúrus vitiensis Seeman, Fl. Vit. 39. 1865.
Gomphandra vitiensis Valeton, Crit. Overz. Olac. 230. 1886.
Lasianthera (*St.*) *Vitiensis* Becc., Mal. **1**: 108. 1877.

Tree, 3–5 m. tall, the branches terete, glabrous; petioles 0.6–0.9 cm. long, sparsely hirsute; lamina ovate or ovate-oblong, 6–10 cm. long, 3–5 cm. broad, thin coriaceous to coriaceous, glabrous, the apex acuminate or subrounded, the base rounded, the midrib sulcate above, prominent below, the veins 10 pairs, oblique and nearly at right angles to midrib, arcuate only at the ends, inconspicuous; the peduncle of the inflorescence 3 cm. long, rhachi sparsely hirsute, calyx indistinctly 5-toothed, cupular, 1.4 mm. in diameter, 0.8–0.9 mm. high, glabrous, except for a few cilia on the teeth; petals oblong, 3–3.5 mm. long, 1–1.1 mm. broad, glabrous, the stamens 2 mm. long in bud, 4–4.4 mm. long after anthesis; pistillate rudiment conical, the functional pistil cylindric, 3 mm. long, the stigma capitate, large; drupe oblong, 1.4 cm. long, 0.6–0.7 mm. wide, the putamen 3-ridged on the convex surface.

Type collection: *Storck* 877 collected at Bureta, Island of Ovalau, Fiji Islands.

Illustration: Seeman, Fl. Vit. pl. 12. 1865.

Specimens seen: Fiji Islands. Ovalau, Bureta, *Storck* 877 (G, isotype). Vanua Levu, Thakaundrove, *Smith* 578 (C, G), *Degener & Ordonez* 14006. Viti Levu. Namosi, *Gillespie* 2653 (C), 3362 (C, G); Nasinu, *Gillespie* 3517 (C, G); Nadarivatu, *Gillespie* 3990 (C, G).

Vernacular name: Duvu.

This species is poorly known and more material is needed to make the

proper comparisons. Only the Degener collection cited above has mature fruits, and this collection is different from the others in possessing coriaceous ovate-oblong leaves. Most of the other collections are either staminate or are sterile. Collections of fruits of this species are especially desirable, and some field notes on leaf variations are needed before the species limits can be finally established.

Medusanthera ovata sp. nov.

Tylecarpus (?) sp. Christophersen, B. P. Bishop Mus. Bull. **128**: 129. 1935.

Arbor ad 15 m. alta; ramis teretibus, puberulis vel glabratis internodiis brevibus; petiolis 1.5 cm. longis, sparse hirsutis; laminis ovatis, 5–7 cm. longis, 3–4.5 cm. latis, subcoriaceis, apice acutis, basi rotundatis, costa supra sulcata subtus prominente, nervis utrinque 5–9, subinconspicuis, margine integris leviter recurvatis; inflorescentiis axillaribus, pedunculo 1–1.4 cm. longo, rhachi sparse hirsuta; calycibus cupularibus 2 mm. diametro, 1.5 mm. altis, glabratis vel ciliatis, petalis oblongis, 4.5 mm. longis, 1.5 mm. latis, glabris, staminibus fertilibus 4.5 mm. longis, filamentis crassis apicem versus dorso et lateribus pilo clavato gerentibus, antheris oblongis, 0.7 mm. longis, ovario conico abortivo. Flores feminini et fructus ignoti.

Type specimen: *Christophersen* 2166 (NY) collected in a swampy place in wet forest, alt. 1300 m., near Matavanu, Savaii, Samoa.

Illustration: Plate 1. Figs. 8–13.

Specimens seen: Samoa. Matavanu, *Christophersen* 2166 (A, NY, US). Mangaloa, *Vaupel* 746 (US).

Christophersen mentioned the differences of this species without giving a technical description of it. Although the species is known only by staminate specimens, it is distinct from the others through the smaller and ovate leaves. It is similar to *M. samoensis* in having clusters of hairs on the dorsal side of the filament below the anther.

MEDUSANTHERA GLABRA (Merr.) Howard, Journ. Arnold Arb. **21**: 469. 1940.

Gomphandra glabra Merr., Phil. Journ. Sci. **17**: 277. 1920.

Tree, 10 m. tall, the branches terete, hirsute to glabrate; petioles 0.9–1.3 cm. long, sparsely hirsute; lamina oblong, 9–17 cm. long, 3.5–7 cm. broad, thin coriaceous, glabrous, the apex acuminate, or rarely acute, the base rounded, the midrib and veins sulcate above, prominent and sparsely hirsute below, the veins 10–11 pairs; peduncle of inflorescence 1–2 cm. long, the rhachi sparsely hirsute; calyx indistinctly 5-toothed, glabrous; petals oblong, 2.8–3 mm. long, 1–1.2 mm. broad, glabrous, filaments of sterile stamens glabrous, filaments of fertile stamens bearing pubescence, fila-

ments to 4 mm. long, slightly flattened, the anther-sacs oblong, slightly diverging at the base, the fertile pistil cylindrical 2.7–3 mm. high, the pistillate rudiment conical, minute; drupe oblong, 7–8 mm. long, 3–5 mm. wide, the sarcocarp fleshy, the putamen weakly 3-ridged on the convex surface.

Type collection: *Merrill*, Phil. Pl. 1628 collected at Yabong, Samar, Philippine Islands.

Illustration: Journ. Arnold Arb. **21**: pl. II. Figs. 8–15. 1940.

Specimens seen: Philippine Islands. Samar, Yabong, *Merrill* Phil. Pl. 1628 (G, US isotypes); Leyte, *Wenzel* 1029 (A, G), 1722 (A, G), 1744 (A, G); Catubig river, *Sablaya* 16 (A), *Ramos* Herb. Phil. Bur. Sci. 24241 (A), 24547 (A).

This species is easily distinguished through the very small fruits. Sterile material or staminate specimens are easily confused with *M. laxiflora*.

MEDUSANTHERA SAMOENSIS (Reinecke) Howard, Journ. Arnold Arb. **21**: 469. 1940.

Tylecarpus samoensis Reinecke, Bot. Jahrb. **25**: 650. 1898; Lloyd & Aiken, Bull. Lloyd Lib. **33**, Bot. Ser. **4**: 65. 1934.

Tree to 6 m. tall, the branches terete, sparsely short hirsute or glabrate; petioles 1–1.7 cm. long, sparsely pubescent; lamina elliptic, 10–17 cm. long, 5–7 cm. broad, thin coriaceous, glabrous, the apex acute or acuminate, the base rounded, the midrib sulcate above, prominent below, the veins 8–10 pairs, oblique at 45-degree angle, almost inconspicuous; peduncle of inflorescence to 3 cm. long, the rhachi sparsely hirsute; calyx cupular, 2.2 mm. diameter, 1.5 mm. high, glabrous or ciliate on the indistinct teeth; petals oblong, 5 mm. long, 2 mm. wide, glabrous; filaments to 3.5 mm. long, the anthers oblong, to 1.3 mm. long; pistillate rudiment conical or ovate, to 1 mm. high, the fertile pistil obovoid, the stigma rugose; drupe oblong, 3–3.5 cm. long, 0.7–1 cm. wide, the base truncate, the apex obtuse, the putamen with a single median longitudinal ridge on the convex surface.

Type collection: *Reinecke* 72a, collected at Vaipouli-Busch, Savaii, Samoa (not seen).

Illustrations: Bot. Jahrb. **25**: t. 13, 1898. Bull. Lloyd Lib. **33**: 65. 1934 (fruit).

Specimens seen: Samoa. Savaii: Alo, *Christophersen* 2312 (NY, US); Salailua, *Christophersen* 3061 (A, NY, US), 3117 (NY); Matavanu, *Christophersen & Humes* 2039 (NY); Safune, *Bryan* 122 (NY). No locality, *Whitmee* s.n. (G); *Laeffe* 1411 (G).

Vernacular names: matamo, tofiga.

This species is easily recognized by the single prominent longitudinal ridge developed on the convex surface of the putamen. All other fruits known in the genus have three or more ridges on the convex surface of the

fruit. The rare occurrence of hair on the dorsal surface of the filament immediately below the anther as found in this species is atypical of *Medusanthera*. Reinecke describes the upper part of the petal as white lanate; however, I have not found such a condition in the material I have examined.

MEDUSANTHERA LAXIFLORA (Miers) Howard, Journ. Arnold Arb. **21**: 470. 1940.

Stemonurus laxiflorus Miers, Ann. Mag. Nat. Hist. II, **10**: 111. 1852.
Platea laxiflora Miers, l. c. 111. 1852.
Gomphandra laxiflora Rolfe, Journ. Bot. **23**: 211. 1885.
Cissus flexuosa Turcz., Bull. Soc. Nat. Mosc. **31**: 115. 1858; Planch. in DC. Monog. Phan. **5**: 624. 1887; Merr. Enum. Phil. Pl. **2**: 420. 1923.

Tree, 10 m. tall, the branches terete, glabrous; petioles 1–1.7 cm. long, sparsely silky hirsute; lamina oblong to lance-oblong, 15–21 cm. long, 5–7 cm. broad, thin coriaceous, glabrous, the apex abruptly acuminate, the base rounded or acute, the midrib and veins sulcate above, prominent below, the veins 10–12 major pairs, 3–7 minor pairs, arcuate; inflorescence peduncle to 3 cm. long, the rhachi hirsute; calyx 2 mm. diameter, 1.5 mm. high, glabrous or ciliate on the indistinct teeth; petals oblong, 4.2–4.4 mm. long, 1.3–1.5 mm. wide, glabrous; stamens to 3.3 mm. long, the filaments thick and fleshy, the filaments of sterile stamens frequently glabrous, the anthers ovate-oblong, 0.7 mm. long; pistillate rudiment conical, to 2.2 mm. long, the fertile pistil cylindrical; drupe oblong, 1.5 cm. long, 0.7 cm. wide, the putamen strongly 3-ridged on the convex surface, the embryo 0.15 mm. long, the albumen bipartite.

Type collection: *Cuming* 891 (Herb. Hook. & Lindl., not seen) collected in the Philippine Islands.

Illustration: Miers, Contrib. Bot. **1**: t. 16. 1851–61.

Specimens seen: Philippine Islands. Mindanao: Surigao. *Wenzel* 2947 (A, C, G), 3224 (A, C, G), 3298 (C), 3365 (C); Pinamalayan. *Ramos* Herb. Phil. Bur. Sci. 41089 (A). Solomon Islands. Bougainville Islands, Konigurii, Buin, *Kajewski* 2178 (A), Karngu, Buin, *Kajewski* 2274 (A). New Guinea: Morobe district, Sattelburg, *Clemens* 100 (A).

Vernacular name: Yemollew.

In the Solomon Islands the branches of this plant are used for making mallets for beating the pith of the sago palm.

Much more material is needed to establish properly the limits of this species.

MEDUSANTHERA CAROLINENSIS (Kaneh.) Howard, Journ. Arnold Arb. **21**: 469. 1940.

Gomphandra carolinensis Kaneh., Fl. Micr. 198, f. 85. 1933, Bot. Mag. Tokyo **47**: 673. 1933.
Tylecarpus carolinensis Kaneh. & Hatus., Bot. Mag. Tokyo **50**: 605. 1936.

Tree 2–3 m. tall, the branches terete, glabrous, olive green in color;

petioles 1.5–2 cm. long, sparsely short hirsute or glabrate; lamina oblong to elliptic-oblong, 14–18 cm. long, 6–9 cm. broad, thinly coriaceous or membranaceous, glabrous, the apex acute or slightly acuminate, the base rounded, the midrib broadly and shallowly sulcate above, prominent and sparsely hirsute below, the veins 8–10 pairs, slightly prominent below, arcuate, free at the ends; peduncles of inflorescence to 3 cm. long, the rhachi appressed hirsute; calyx cupular, 1.5 mm. diameter, 1 mm. high, indistinctly 5-toothed, ciliate on the teeth; petals oblong, 3.8–4.2 mm. long, 1.6 mm. wide, glabrous; filaments of staminate flowers 3–3.8 mm. long, the anthers oblong-ovoid, 1 mm. long, the pistillate rudiment ovoid-conical, 1 mm. high; female flowers not known; drupe oblong, 2 cm. long, 1 cm. wide, shining olive green in color, the putamen strongly 3-ridged on the convex side.

Type collection: *Kanehira* 1908 B from Korror, Palau Island, Caroline Islands.

Illustration: Bot. Mag. Tokyo **50**: 606. 1936.

Specimens seen: Caroline Islands. Palau: Korror, *Kanehira* 1882 (NY), 1908 B (NY isotype); Coral Islands, *Kanehira* 2473 (NY); Aimiriik, *Kanehira* 4578 (A). Solomon Islands. San Cristoval Island, Kira Kira, *Brass* 2718 (A). Owa Raha Island, *Brass* 3135 (A).

This is a poorly marked species but can be distinguished on the elliptic-oblong lamina and the arcuate veins which are free at the ends.

SPECIES EXCLUDED

Medusanthera australis Howard equals *Irvingbaileya australis* (White) Howard.

Tylecarpus australis White equals *Irvingbaileya australis* (White) Howard.

Stemonurus Merrittii Merr. equals *Codiocarpus Merrittii* (Merr). Howard.

Tylecarpus Merrittii Sleumer equals *Codiocarpus Merrittii* (Merr.) Howard.

Tylecarpus andamanicus Sleumer equals *Codiocarpus andamanicus* (Kurz) Howard.

Studies of the Icacinaceae. VIII. Brief Notes of Some Old World Genera

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This paper contains further notes on the application of the name *Stemonurus* Blume, descriptions of two new species of *Urandra* Thwaites and also two of *Platea* Blume, as well as the first description of the fruits of the genus *Pittosporopsis* Craib.

Specimens cited are from the herbaria of the Arnold Arboretum (A), the University of California (C), and the New York Botanical Garden (NY). I am grateful to the directors and curators of these herbaria for the use of the materials.

The recent work of Sleumer (*Notizbl.* **15**: 238. 1940), Howard (*Journ. Arnold Arb.* **21**: 461. 1940), and Merrill (*Journ. Arnold Arb.* **23**: 176. 1942) has shown that there exists some confusion regarding the correct application of the name *Stemonurus* Blume. An attempt is made here to clarify this problem.

Blume published generic descriptions under the name of *Stemonurus* in 1825 and again in 1849. The genus as originally established consisted of four species, three in one section and a single species in a second section. Blume did not indicate which of these species was the type of the genus. Later, *Stemonurus frutescens*, the single species of the second section, was selected as the type of a new genus, *Anacolosa*, by Blume himself. Of the remaining three species, *Stemonurus pauciflorus* and *S. javanicus* have been considered identical and the remaining species *S. secundiflorus* belongs to an entirely different genus. These two generic units are recognized by all workers, and their limits (Howard l.c.) do not enter into the present discussion. The immediate problem, however, is to which of these generic units does the name *Stemonurus* apply.

Blume's original description is transcribed below. In this description I have italicized all the characters which apply only to the generic unit represented by *S. pauciflorus* and *S. javanicus*. All the characters applying only to the generic unit represented by *S. secundiflorus* have been placed in small capitals, and finally, all characters which could apply to either of the groups are in a normal print.

Stemonurus Blume, ex Bijdr. **13**: 648. 1825.

Flores HERMAPHRODITI, *ex abortu interdum dioeci*. Calix brevis, integerrimus, aut obsolete dentatus. Petala 5 rarius 6, *inferne coalita*. Stamina 5 rarius 6, hypogyna; filamenta petalis alterna compressa, singula ad apicem munita fasciculo villorum; antherae biloculares, introrsae. *Ovarium oblongum*, 1-loculare, 2-ovulatum; ovula pendula. *Stigma sessile, obtusum. Drupa baccata, umbilicata*, nucleo 1-spermo. Embryo inversus, parvus, ad apicem albumini immersus.

Arbores seu frutices, foliis alternis integerrimis, floribus parvis axillaribus spicatis.

The only character in this description which applies solely to the genus represented by *S. secundiflorus* is the "flores hermaphroditi" and for this an alternate character is mentioned. It is evident that the majority of the limiting characters apply only to *S. pauciflorus* and *S. javanicus* and that Blume based this generic description on those two species. The critical generic characters apply only to those species and not to *S. secundiflorus*. However, Koorders and Valeton (Boomsort. Java **5**: 145. 1900) picked *S. secundiflorus* for the type species, commenting, "Genus *Stemonurus* Bl. cuius species typica *S. secundiflorus* a Blume in Tab. XLV Mus. Bot. optime delineata est." Thus Koorders and Valeton were more impressed by the illustration of *S. secundiflorus* which Blume published fifteen years later than they were by the original generic diagnosis. The second generic description differs in many ways from the original one, and considering it in the same manner one finds a different generic concept indicated in it.

Stemonurus Blume, ex Mus. Bot. Lugd. Bat. 1: 249. 1849.

Flores HERMAPHRODITI v. *abortu dioeci*. Calyx parvus, cupularis, truncatus v. denticulatus, immutato-persistens. Corollae petala 5 v. 4, hypogyna, *inferne coalita*, praefloratione valvata. Stamina 5 v. 4, ad basin petalorum inserta et iis alterna, plerumque exserta; filamenta carnosa, compressa, singula apice fasciculo villorum munita; antherae filamentorum apici adnatae, introrsae, ovatae biovulares, latere dehiscentes. OVARIUM CONICUM v. *cylindricum*, AD BASIN DISCO BREVI ANNULARI CINCTUM, uniloculare. Ovula 2, ex apice loculi pendula anatropa. STIGMA TERMINALE, SIMPLEX v. CONICUM, SULCATUM. Drupa *baccata*, NUCLEO FIBROSO, monospermo. Semen inversum. Embryo in apice albuminis carnosi orthotropum; COTYLEDONES BREVES, OBTUSAE; radicula cylindrica, obtusa, supera. Arbores v. frutices, in Archipelago indico crescentes; foliis alternis, petiolatis, oblongis, integerrimis, laevibus, glabris, venosis v. SUBAVENIIS; floribus parvis, flavo-viridulis, odoratissimis, in RACEMOS v. spicas v. CYMAS SAEPA UNILATERALES DISPOSITIS; fructibus purpureis.

This second generic description published by Blume is obviously based primarily on *S. secundiflorus* and agrees with the accompanying illustration of that species.

Koorders and Valeton made an unfortunate error in picking a type species which does not fit the original generic description. It is true, as Merrill (l.c. 177) has pointed out, that the International Rules do give the worker who revises a group the opportunity of selecting a type species, but if the International Rules are to be meaningful in such problems as this, then the author should select as a type species one that conforms with the generic concept in the original description and should not be influenced by later changes in that description or by subsequent illustrations. In the second publication Blume did not merely alter or amplify his original description but described an entirely different genus. I do not believe it is correct to follow the rules to the letter in this case and agree with Koorders and Valeton, but I do believe that one should reselect a type species for *Stemonurus*. The species selected for the type should agree with the original description. For that reason the name *Stemonurus* should be reserved for the generic unit represented by *S. pauciflorus* and *S. javanicus*, of which

the type species is *Stemonurus javanicus*. Under this interpretation *Gomphandra* Wallich ex Lindley (1836) is a later homonym of *Stemonurus*. It is also necessary to find a new name for the generic unit containing *S. secundiflorus*, and the next available name is *Urandra* of Thwaites. The type species of this genus is *U. apicalis* Thwaites.

It is not necessary to make many new combinations or new names as has been suggested (Merrill l.c.). Only the species recently described by Sleumer and Merrill under the name *Gomphandra* need to be transferred.

The name *Urandra* has been used only for those species having characters of *U. secundiflorus*. The name *Stemonurus* has been used, more commonly, to represent species with the characters of *S. javanicus*. Certainly the correct usage of these two names is less confused than would be the alternate suggestions of Sleumer and Merrill.

A synoptic treatment of the essential characters of *Stemonurus* and *Urandra* as well as others associated with them will be found in an earlier paper (*Journ. Arnold Arb.* **21**: 463–4. 1940). For a complete treatment of *Medusanthera* see my paper on this genus in *Lloydia* **6** (2): 133–143, 1943.

Recently I have seen some additional material of the genus *Urandra*. Included were the two new species described below. A complete treatment of *Urandra* can not be offered until the material in European herbaria is again available, as type materials are lacking in America and many species are not represented in the collections in this country.

The genus *Urandra* contains plants which have axillary inflorescences which are pedunculate umbels. The branches of the umbels may be very short or practically nonexistent, so that the inflorescence appears as a head or capitate cluster of flowers, or the branches may be long. In the latter instance the flowers may be secund along the branches of the inflorescence or they may be aggregated in small clusters at the tips of the branches. The species may be grouped on the basis of the form of the inflorescence as follows: (1) species in which the flowers are secund on elongate branches of the umbel: *U. secundiflora*, *U. lanceolata*, *U. scorpioides*, *U. Ridleyana;* (2) species in which the inflorescence is subcapitate or the flowers are borne on very short branches of an umbel: *U. apicalis*, *U. labuanensis*, *U. malaccensis*, *U. evenius*, *U. grandifolia*, *U. dolichophylla;* (3) species in which the flowers are capitate on elongate branches of the umbel: *U. elliptica*, *U. Gitingensis*, *U. monticola*, *U. umbellata*, *U. Hallieri*, and the following two new species.

Urandra Brassii sp. nov.

Arbor: ramulis teretibus glabris, internodiis 2–3 cm. longis; petiolis 10–15 mm. longis anguste sulcatis; laminis foliorum lanceolato-ellipticis, 13–17 cm. longis, 4.5–6 cm. latis, coriaceis glabris, apice acuto vel acuminato, basi acuta, costa supra sulcata, subtus prominente, nervis lateralibus

utroque latere 12–14, supra vix prominentibus subtus inconspicuis, margine revoluto; inflorescentiis axillaribus, pedunculis 2–3 cm. longis, bracteatis ramis umbellatis 4–6, ad 1 cm. longis, ad apicem 3–5 flores gerentibus; calycis cupulis 2.4 mm. diametro, 1.8 mm. altis, sparse puberulis, lobis 5 late triangularibus; petalis oblongis 4 mm. longis, 1.5 mm. latis glabris; staminibus 3.5–4.5 mm. longis, antheris ovato-oblongis, 1 mm. longis, filamentis apicem versus dense barbatis; pistillo conico, 3.7 mm. alto, glabro; fructu ignoto.

Type specimen: *Brass* 7421 (A) collected at Oroville Camp, Fly River, thirty miles above D'Albertis Junction. British New Guinea.

Illustration: Plate 1, figs. 1–2.

This plant was growing in the forest substage. The bark was pale brown, laminated and suberose, and longitudinally fissured. The flowers were white and fragrant. The pubescence on the upper portions of the filaments was long and dense. Hairs on the ventral surface only equal the anther, while the hairs on the dorsal surface of the filament are almost as long as the stamen.

The secondary veins of the leaves are noticeable only on the ventral surface. There are 12–14 pairs of veins which approach the leaf margin and other less distinct veins in between which are very short. The dorsal leaf surface is perfectly smooth.

Urandra Brassii is distinct from the other species of *Urandra* which have the flowers clustered at the ends of the umbellate branches by possessing leaves which are acute or attenuate at both ends. The leaves are larger than those of *U. nitida* and do not have a shining ventral surface. The peduncle of the inflorescence is characteristically twice as long as the petiole, easily separating *U. Brassii* from *U. nitida*. The minute ovate bracts at the apex of the peduncle which subtend the branches of the inflorescence are deciduous very early.

I have seen a collection by Kloss 19043 (A, NY) from Bettotan near Sandakan, British North Borneo, which may also be referred to this species. The Kloss specimen has identical leaves, but the inflorescences are very immature and are shorter than the petiole in this collection.

Urandra nitida sp. nov.

Arbor, 10–13-metralis; ramulis teretibus, leviter longitudinaliter striatis, aliquando squamiferis vel resinaceis; petiolis 5–7 mm. longis, leviter sulcatis, glabris; laminis oblongis, 5–8.5 cm. longis, 2–3 cm. latis, coriaceis, glabris, supra nitidis, apice acuto vel acuminato (acumene ad 3 mm. longo, obtuso), basi acuta, costa supra sulcata subtus prominente, nerviis lateralibus foliorum utroque 12, inconspicuis, margine revoluto; infrutescentibus axillaribus pedunculis 3–6 mm. longis, ramulis 1–2, ad 5 mm. longis; fructu drupaceo obloideo, 3.5–3.7 cm. longo, 1 cm. diametro, calyce persistente.

PLATE 1. Figs. 1–2, *Urandra Brassii* Howard (Brass 7421). Figs. 3–6, *Urandra nitida* Howard (Haniff 152).

Fig. 1, habit of *U. Brassii* ×½; fig. 2, functional pistil ×6; fig. 3, habit of *U. nitida* ×½; fig. 4, diagrammatic cross-section of a mature drupe; fig. 5, side view of a mature seed ×½; fig. 6, embryo ×½.

Type specimen: *Haniff* 152 (C) collected at Ayer Etam Reservoir, Penang.

Illustration: Plate 1, figs. 3–6.

This plant was collected at an elevation of 500 ft. It was in fruit in January.

This species belongs to that group in which the flowers are clustered at the ends of the branches of the umbel. The peduncle is very short and seldom more stout than the petioles. Only one or two branches were developed to the infrutescence in the specimens seen, but scars of at least two others were noticed; thus, in the flowering condition, two to four branches might be expected to the inflorescence. I have not seen flowers of this species. The fruits are articulated below the 5-lobed calyx, which is minutely puberulous on the lobes. Remnants of the annular skirt or thin disc which is present at the base of the conical pistil and is characteristic of *Urandra* are present in the mature drupe. The drupe is elongate obloid tapering slightly to the apex and the base. The apex is slightly curved so that the style is off center. The fruit is apparently two-colored when fresh, as the bottom half has a darker hue than the top.

The tapering acute apex of the leaves, with the small and very shining lamina, makes *Urandra nitida* distinct among those species having the flowers capitate on the branches of the umbel.

The species of Platea which have already been described fall into two groups, those with a pubescence on the ovary and those with the ovary glabrous. Careful re-examination of the types and new descriptions are very much desired for several species not clearly defined. Two new species are described here, one with a pubescent ovary and one with a glabrous ovary.

Platea hainanensis sp. nov.

Arbor, ad 18 m. alta, trunco ad 21–31 cm. diametro, ramulis teretibus, dense ferrugineo-lepidoto-stellatis, ramis teretibus sparse ferrugineo-lepidoto-stellatis; petiolis 2.3–3.5 cm. longis, supra leviter sulcatis, sparse lepidoto-stellatis, laminis lanceolato-oblongis vel lanceolato-ellipticis, 13–19 cm. longis, 5.5–9 cm. latis, chartaceis vel tenuiter coriaceis, juvenilibus ferrugineo-lepidoto-stellatis, ad maturitatem supra glabris subtus glabratis, apice acuminatis (acumene ad 1.5 cm. longo), basi acutis, margine integra, plana, costa supra sulcata, subtus prominente, nervis secundariis utrinsecus 8–9, subtus prominentibus, obliquis vel arcuatis, ad marginem leviter anastomosantibus, persistenter lepidoto-stellatis; inflorescentiis masculinis axillaribus, 5–7 cm. longis, ramis dense ferrugineo-stellato-tomentosis, bracteatis, floribus glomerulatis, calyce 1.5 mm. diametro, 1 mm. alto, 5-lobato, lobis ovatis, 0.4–0.7 mm. longis, 0.3–0.5 mm. latis, ciliatis, corolla 5-lobata, lobis 1.6 mm. longis, 1.0 mm. latis, glabris, apice

inflexis, staminibus tubo insertis, antheris oblongis, 0.4 mm. longis, filamentis 0.1 mm. longis, glabris; pistillo rudimentari, conico, glabro, 0.1 mm. alto; floribus femineis ignotis; infrutescentia ad 1.5 cm. longa, ramis bracteatis, dense lepidoto-stellatis; drupo solitario, oblongo, 3.8–4 cm. longo, 1.6–2 cm. diametro, apice basique attenuato, pericarpio brunneo aut flavo, putamine 1–1.5 mm. crasso, intus levi, extus reticulato, semine solitario, apice pendulo, ad 3 cm. longo, embryone 5 mm. longo, cotyledonibus lanceolatis, 3 mm. longis, endospermio copioso.

Specimens seen: Hainan. Kan-en district, Chim Fung Ling near Sam Mo Watt village, *Lau* 3808 (A); Boting, *Lau* 28304 (A); Kumyun, *Lau* 27855 (A type); *Liang* 64940 (A); Foo Lung, Sup Man Ta Shan, *Liang* 69704 (A); Yao Shan, *Wang* 39933 (A).

Illustration: Plate 2.

Platea hainanensis is similar to *P. excelsa* in the shape of the lamina. It differs in having a lepidote-stellate pubescenec on the ovary and the drupe, longer petioles, and fewer veins to the leaves. The pubescence also distinguishes *P. hainanensis* from *P. latifolia*, as do the more lanceolate leaves and the shorter female inflorescence, which is only one-flowered. *Platea hainanensis* may be distinguished from *P. philippinensis* through the lance-oblong leaves with abruptly acuminate apices and broader bases as well as through the less numerous veins to the leaves and the larger fruits.

Platea montana sp. nov.

Arbor 30 m. alta, trunco ad 49 cm. diametro, ramulis striatis, dense ferrugineo-lepidoto-stellatis, ramis teretibus, glabratis, petiolis crassis, 1.3–1.6 cm. longis, supra sulcatis, lepidoto-stellatis, laminis oblongis, 5.5–8 cm. longis, 2–3.5 cm. latis, juvenilibus dense ferrugineo-lepidoto-stellatis, ad maturitatem supra glabratis, subtus sparse pubescentibus, apice rotundis vel obtusis, basi acutis, marginibus vix revolutis, costa supra sulcata, subtus prominente, nervis secundariis utrinsecus 6–8, obliquis, ad marginem arcuatim inconspicue anastomosantibus; inflorescentiis masculinis spicatis, 3 4.5 cm. longis, bracteatis, ramulis leviter ferrugineo-stellato-tomentosis, floribus glomerulatis, calyce 5-lobato, tubo 0.5 mm. alto, lobis imbricatis, ovatis, 0.5–0.7 mm. longis, 0.4–0.5 mm. latis, ciliatis vel rarius stellato-tomentosis; corolla 5-lobata, tubo 0.5 mm. alto; lobis oblongis, 2 mm. longis, 1 mm. latis, glabris, apice inflexis; staminibus glabris, tubo insertis, antheris ellipticis, 0.6 mm. longis, filamentis 3 mm. longis, glabris; pistillo abortivo, conico, glabro, 0.1 mm. alto; inflorescentiis femineis ad 1 cm. longis, ramis dense stellato-tomentosis, bracteatis 1–2-floris, calyce 5-lobato, lobis ciliatis et stellato-tomentosis, petalis et staminibus nullis; pistillo cylindrico obconico, 2.5 mm. alto, 2 mm. diametro, glabro, stigmate capitato, rugoso, loculo solitario, ovulis 2, collateralibus, pendulis anatropis; drupa matura ignota.

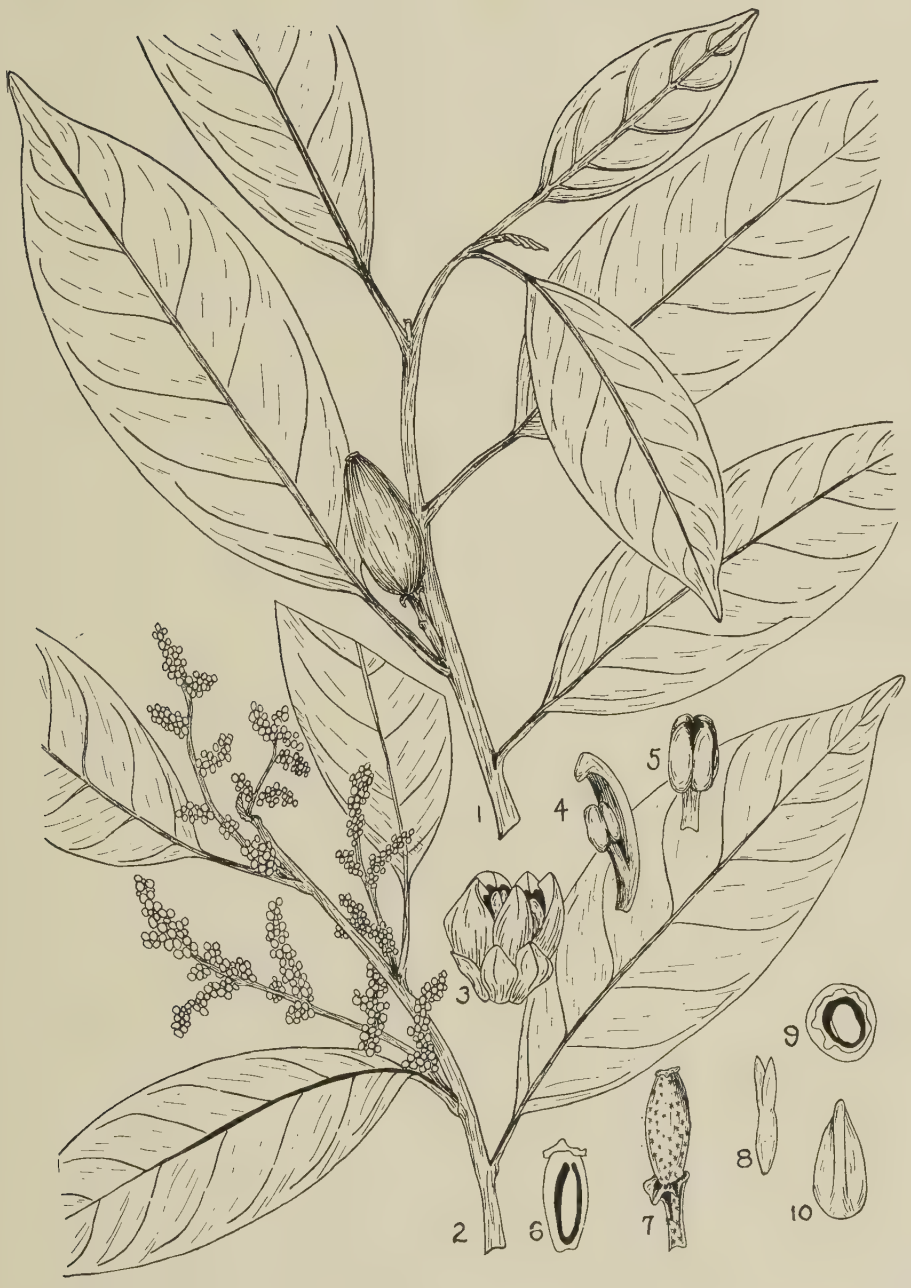

PLATE 2. *Platea hainanensis* Howard. (Figs. 1, 6–10 Lau 27855 type. Figs. 2–5, Liang 64940.) Fig. 1, habit of pistillate branch ×½; fig. 2, habit of staminate branch ×½; fig. 3, staminate flower at anthesis ×8; fig. 4, lateral view of petal showing attachment of the stamen ×12; fig. 5, adaxial view of single stamen ×5; fig. 6, diagrammatic longitudinal section of a pistil; fig. 7, young fruit ×½; fig. 8, embryo ×3; fig. 9, diagrammatic cross-section of a mature fruit; fig. 10, side view of a seed ×¼.

Specimens seen: Netherlands New Guinea. Bernhard camp, Idenburg river, *Brass & Versteegh* 11910 (A type), 12554 (A); Angi Arfak Mts., *Kanehira & Hatusima* 14098 (A).

Illustration: Plate 3.

Platea montana is very distinct on its small oblong leaves and short inflorescences. The plants, however, are the largest trees reported in this genus. They occur in primary forests at altitudes of 1200–2200 m. Brass and Versteegh describe the thin bark as gray or dark brown and shallowly fissured or rough. The wood is red-brown and the flowers are light green. The young fruits are green.

Platea montana is similar to *P. oblonga* which Valeton mentioned but did not describe completely. Sleumer has suggested that *P. oblonga* may not belong in this genus since it lacks the characteristic stellate-lepidote pubescence on the leaves. I have not seen mature fruits of *P. montana* and so can not make a comparison with the characters given by Valeton.

Platea latifolia as described by Koorders and Valeton has a densely villose ovary. This pubescence consists of simple hairs and is lost very early. Only a few scattered hairs may be found on the mature fruit. Recently Sleumer (l.c.) has suggested that *P. philippinensis* and *P. Riedeliana* belong in synonymy with *P. latifolia*. This is not likely, as in *P. philippinensis* the ovary possesses a lepidote-stellate pubescence which is usually persistent on the mature drupe. In addition, there are differences in the abundance of the pubescence of the leaf, the shape of the blade, and the venation of the leaf. I have not seen any material of *P. Riedeliana* which Beccari described from Biliton, and no mention is made of the presence or absence of pubescence in the original description; nevertheless, the leaf apex is described as round, obtuse, or subemarginate, not acuminate as in *P. latifolia*. I do not believe these two species are synonymous with *P. latifolia*.

Recent collections by Wang in Yunnan province of China have supplied fruits of *Pittosporopsis Kerrii* Craib which had not been described in earlier literature. The two collections, *Wang* 78092 (A) (from Youlouh shan, Che-li Hsien made in mixed forests at an altitude of 1100 m.) and *Wang* 79188 (A) (from Jah-leei, Che-li Hsien also from mixed forests at 1200 m.), have five fruits. These are ovoid and slightly flattened, 2–2.5 cm. long, 2 cm. wide, and 1.5–1.7 cm. thick. The pericarp is thin and tenuous. The putamen is uniformly thin, 0.4 mm. thick, and essentially smooth inside and out. There is a prominent vascular strand running lengthwise around the fruit. A very short projecting style is present at the apex. The calyx persists and is slightly accrescent to 6 mm. in diameter. The dehiscence of the fruit occurs at the articulation at the base of the calyx.

A single seed, pendent from the apex of the locule, is present. The endo-

PLATE 3. *Platea montana* Howard. (Figs. 1, 3–6, 9 Brass & Versteegh 12554. Figs. 2, 7–8, 10 Brass & Versteegh 11910 type.)

Fig. 1, habit of staminate branch $\times\frac{1}{2}$; fig. 2, habit of pistillate branch $\times\frac{1}{2}$; fig. 3, adaxial view of a petal showing position of stamen attached to corolla tube $\times 14$; fig. 4, lateral view of a stamen $\times 6$; fig. 5, side view of corolla showing the short tube $\times 8$; fig. 6, portion of staminate inflorescence $\times 8$; fig. 7, side view of a pistil $\times 9$; fig. 8, diagrammatic longitudinal section of a pistil; fig. 9, side view of calyx of staminate flower $\times 6$; fig. 10, portion of the pistillate inflorescence $\times 8$.

sperm is copious and is ruminated similar to some species of *Gonocaryum* and various genera of the Phytocreneae. The embryo is slightly curved. The cotyledons are large, ovate, 9 mm. long and 7.5 mm. wide, and are not superposed. The radicle is cylindrical, to 5.5 mm. long, and is enlarged at the base.

Wang reports the fruits to be green or greenish white when fresh. The dried specimens are a light brown color.

Advance in Phylogenetic Position in the Cryptogams as Indicated by Their Fats

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It has already been determined that seed fats of tropical angiosperm plant families have lower iodine values, lower molecular weights and higher melting points than the seed fats of temperate angiosperm plant families. It has likewise been shown that when seed fats of these plant families are first separated according to climate of habitat, that the higher the plant family is in evolutionary position the more likely it is to form seed fats with large iodine numbers, higher molecular weights and lower melting points. There are also indications of an increase in the number of acids in seed fats with advance in evolutionary position.[1]

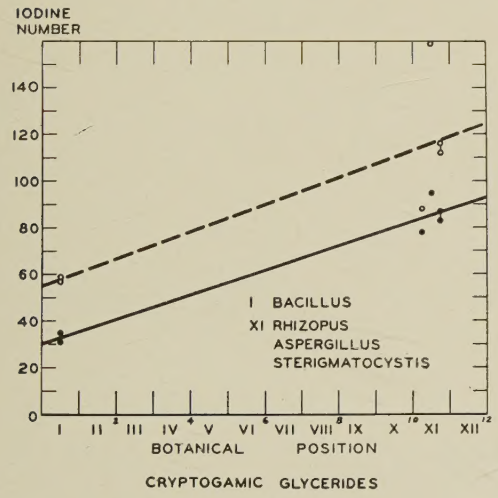

Fig. 1. The relationship between iodine values of fats and botanical position of Timothy grass bacillus, *Rhizopus nigricans*, *Aspergillus niger*, and *Sterigmatocystis nigra* when grown at high and low temperature levels. The solid points indicate the iodine values of fats produced at lower temperatures. The open circles indicate those produced at higher temperatures. The solid line (lower temp. products) and the broken line (higher temp. products) indicate the upward trends of the iodine values with increase in evolutionary position of the producing organisms. Data from Table 1.

It is of interest, therefore, to find experimental evidence in favor of a similar situation in the lower plants—cryptogams. In Table 1 and Fig. 1 five organisms are listed in evolutionary sequence. These are (Engler and Prantl classification) Division I, Schizophyta, Timothy grass bacillus; Division XI, Eumycetes, Class 1, Phycomycetes, *Rhizopus nigricans;* Class 2, Ascomycetes, *Aspergillus fischeri, A. niger;* and Class 4, Basidiomycetes, *Sterigmatocystis nigra.* From these results it is apparent that the fats with the highest iodine values are produced at the lowest temperature, and in the case of *Aspergillus niger* the fat produced at a temperature intermediate between the highest and the lowest has also an intermediate iodine value. The temperature and mean iodine values are respectively: for I. Timothy grass bacillus 14° (iod. val. 58), 35° (33); for II. *Rhizopus*

[1] J. B. McNair, Amer. J. Bot. **16:** 832–841, 1929; **21:** 427–452, 1934; Phytologia **2:** 33–49, 1941; Science, **94:** 422, Oct. 31, 1941.

TABLE 1

Plant	Temperature (degrees C.)	Reaction Time (days)	Molecular Weight (mean)	Iodine Number of Fat	Reference[2,3,4]
I. Division, Schizophyta					
Timothy grass bacillus...	14°			57. – 59.	Terroine et al.
	35°			31. – 35.	" " "
XI. Division, Eumycetes					
1. Class, Phycomycetes					
Rhizopus nigricans...	12°	30	289	87.2– 88.7 (mean 88.)	Pearson et al.
	25°	10	288	79.	" " "
		13	287	77.3 (mean 78.)	" " "
2. Class, Ascomycetes					
Aspergillus fischeri...	20°	16		93.	Frill et al.
	37°	12		88.	" " "
Aspergillus niger.....	18°	17	302	146.7–153.6	Pearson et al.
		56	323–330	145.9–150.2 (mean 149)	" " "
	25°	10	287	124.	" " "
		14	304	132.5	" " "
		17	290	131.3	" " "
		35	287	127. (mean 129)	" " "
	35°	6	293	92.1	" " "
		7	285	92.3	" " "
		9	290	99.9 (mean 95.)	" " "
4. Class, Basidiomycetes	17°			112. –116.	Terroine et al.
	35°			83. – 87.	" " "

[2] L. K. PEARSON AND H. S. RAPER, Biochem. J. **21**: 875–879, 1927.

[3] E. F. TERROINE, R. BONNET, G. KOPP AND J. VECHOT, Bull. soc. chim. biol. **9**: 605–619, 1927.

[4] E. A. PRILL, P. R. WENCK AND W. H. PETERSON. Biochem. J. **29**: 21–33, 1935.

nigricans 12° (88), 25° (78); for III. *Aspergillus fischeri* 20° (93), 37° (88); for IV. *A. niger* 18° (149), 25° (129), 35° (95); and for V. *Sterigmatocystis nigra* 17° (114), 35° (85).

There are also indications that the fats with the highest iodine values and highest molecular weights are also produced by the plants highest in evolution when these plants are grown at comparative temperatures e.g., I. 14° (iod. val. 58), II. 12° (88) (mol. wt. 289), III. 20° (93), IV. 18° (149) (m.w. 323), and V. 17° (114) or I. 35° (33), II. 35° (78) (m.w. 287), III. 37° (88), IV. 35° (95) (m.w. 290) and V. 35° (85). Conversely (as shown by the above figures) there are indications that the fats with the lowest iodine values and lowest molecular weights are produced by the plants lowest in evolution when these plants are grown at comparative temperatures.

It is hoped that the publication of these relationships between temperature, iodine value and phylogenetic position will stimulate the analysis of more fats from spores and seeds of plants grown at controlled temperatures.